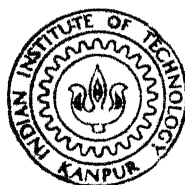


# SOME PROBLEMS IN ENVIRONMENTAL BIOLOGY

By

R. NALLASWAMY



DEPARTMENT OF MATHEMATICS

AN INSTITUTE OF TECHNOLOGY KANPUR

MARCH, 1981

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# SOME PROBLEMS IN ENVIRONMENTAL BIOLOGY

A Thesis Submitted  
in Partial Fulfilment of the Requirements  
for the Degree of  
DOCTOR OF PHILOSOPHY

20259

By  
R. NALLASWAMY

*to the*

DEPARTMENT OF MATHEMATICS

INDIAN INSTITUTE OF TECHNOLOGY KANPUR

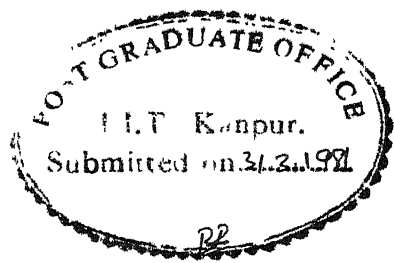
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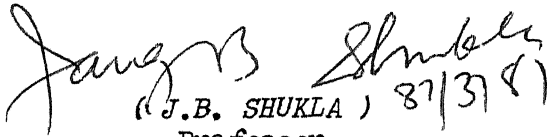
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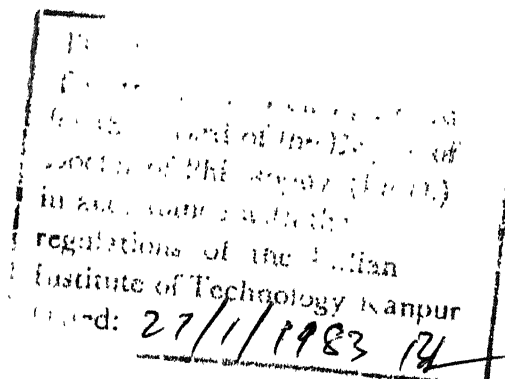


CERTIFICATE

This is to certify that the matter embodied in the thesis entitled 'SOME PROBLEMS IN ENVIRONMENTAL BIOLOGY' by Mr. R. Nallaswamy for the award of Degree of Doctor of Philosophy of the Indian Institute of Technology, Kanpur, is a record of bonafide research work carried out by him under my supervision and guidance. The results embodied in this thesis have not been submitted to any other University or Institute for the award of any degree or diploma.

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7) Mathematical Modelling	B
8) Numerical Solution of Partial Differential Equations	A

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2. *Environmental pollution from a time dependent point source.*
3. *Reversible absorption of a pollutant from an area source in a stagnant fog layer.*
4. *Effects of dispersal on stability of two species system with mutualistic interactions and functional response.*
5. *Effects of dispersal on stability of prey-predator system with functional response.*
6. *Effects of dispersal on stability of two competing species system with functional response.*
7. *Effects of dispersal on stability of gonorrhea epidemic model.*

( R. NALLASWAMY )

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## CHAPTER I

### GENERAL INTRODUCTION

#### 1.1 INTRODUCTION

Environmental Biology deals with the study of evolution and co-existence of biological species in the surrounding environment. Generally, the evolution of the species depends on many factors such as over-crowding, age structure, past population size, sources of food supply, interactions with other species, topographical, ecological and environmental conditions in the habitat including seasonal and climatic variations. Due to rapid industrialisation and deforestation, the environment and ecology of the earth has been deteriorating continuously leading to the extinction of rarer species belonging to the animal and plant kingdom and creating health hazards in the form of pollution to various living beings. Because of various undesirable factors which arise due to ecological and environmental gradients in natural habitats, the tendency of the species, therefore, is to migrate from unfavourable to favourable regions for their survival. In general, migration of the species in the habitat can be studied by identifying it with convective and dispersive processes. One of the important aspects in theoretical biology, therefore, is to investigate how convective and dispersive migration affect



the stability and persistence of model communities of interacting species.

Keeping the above in view, the following problems have been studied in this thesis.

- (i) Pollutant dispersion from time dependent point and area sources.
- (ii) Effects of convective and (or) dispersive migration on the linear and nonlinear stability of systems of two interacting species with functional response in finite and infinite habitats with ecological and environmental gradients in and around it.
- (iii) Effects of dispersal on the stability of gonorrhea epidemic model.

We may note that the available literature regarding the above is rather extensive wherein a large number of important ideas have been brought to focus. We shall, therefore, review only the most pertinent researches from the point of view of the problems taken up in this thesis.

## 1.2 ENVIRONMENTAL POLLUTION

Air pollutants, such as sulphur dioxide, carbon dioxide, etc., are dispersed in the environment by the process of molecular diffusion which arises due to changes in concentration and depends upon various factors such as types and number of sources, stack heights, meteorological conditions

and the topography of the terrain. A great deal of attention has been devoted to study the molecular diffusion process by using the well known Fick's law of diffusion and these have been well documented by Crank [22], Deininger [24], Pasquill [92], Scorer [108], Stern [124] and Sutton [125]. Hoffert [56] has presented an excellent review which deals with scientific and engineering aspect of air pollution by taking into account the environmental factors such as wind turbulence, stability of atmosphere and atmospheric chemistry.

Using Gaussian plume and other models, several investigators have studied the dispersion of air pollutants due to a point source under various conditions, Cleary et al. [17], Fay and Rosenzweig [32], Gupta and Gupta [46], Horst [59], Lamb and Seinfeld [67], Lubini and Tirabassi [76], Pasquill [92], Pattle [93], Peters and Klinzing [94], Peters and Richards [95], Ragland and Dennis [99], Ragland [100], Smith [119]. Although the Gaussian plume model is advantageous due to its simplicity in calculations, it does not represent the real system in a complex terrain and changing meteorological conditions as it ignores the boundary layer effect near the ground where topography plays an important role, Hoffert [56], Saffman [106]. Fay and Rosenzweig [32] have discussed a steady state two dimensional diffusion model suitable for predicting ambient

air pollutant concentrations averaged over a long period of time and resulting from the long distance transport of pollutants. In reality, the dispersion from a point source should be studied by considering a three dimensional diffusion equation with variable diffusivity and wind velocity, Lamb and Seinfeld [67]. Analytical solutions of such equations for elevated point source have been obtained under various conditions, Ermak [30], Peters and Klinzing [94]. Using numerical techniques, Ragland and Dennis [99] have studied the dispersion of a pollutant from an elevated point source by taking topographical effects into account. They have considered various forms of wind speed and eddy diffusivity in determining the concentration profiles. Recently, Lupini and Tirabassi [76] have proposed a modified Gaussian model that gives the geometric features of the solutions of a two dimensional steady-state advective-diffusion equation under a heightstructured atmospheric boundary layer condition. Peters and Richards [95] have developed a procedure to study dispersion from point sources with simultaneous reversible chemical reactions. The validity of the procedure necessitates the chemical reactions to be rapid enough relative to the transport so that local chemical equilibrium is achieved at receptor site.

In recent years, the dispersion of pollutant from a line source has been investigated by many workers, Chock [14],

Dilley and Yen [27], Liu and Seinfeld [75], Sharma and Myrup [113], Walters [130]. In particular, Walters [130] has studied the dispersion by considering uniform air velocity and taking eddy-diffusivity as a linear function of height. Dilley and Yen [27] have performed a more general study of dispersion from a cross wind line source by taking power law models of horizontal and vertical velocities where diffusivity also varies as a power law profile. A comparison between this and trajectory model has also been made, Liu and Seinfeld [75], Sharma and Myrup [113]. Chock [14] has proposed a simple line source model to describe the down-wind dispersion of pollutants near the roadway. It is potentially more accurate than the existing Gaussian models especially under adverse meteorological conditions when the plume becomes important. An attempt has also been made by Calder [8] to examine the general structure of multiple source plume models for urban air pollution.

Investigations relating to the study of dispersion from area sources have also been carried out by several workers, Draxler [28], Egan and Mahoney [29], Martin [78], Omstedt and Rodhe [91], Ragland [98], Stern [124]. Liu and Seinfeld [75] have compared the validity of grid and Trajectory models of urban air pollution due to area sources. Using similarity solutions, Gifford and Hanna [35]

have analysed the diffusion from an area source for power law variations of velocity and eddy diffusivity. A study of atmospheric transport of pollutants from an area source has been carried out by using integral method, Lebedeff and Hameed [68]. Nunge and Sankar Subramanian [88] have studied the atmospheric dispersion of gaseous pollutants from a continuous area source using generalized dispersion theory, Sankar Subramanian and Gill [107]. Draxler [28] has considered a simple sector-average Gaussian dispersion model to develop long term average concentrations. The model accounts for day/night variations in mixing depth as well as stability changes with time, wind speed adjustment to stack height and a more realistic treatment of calm winds.

Chu and Seinfeld [16] have derived a comprehensive mathematical model to study the dynamic behavior of urban aerosols by considering the effects of factors such as pollutant reaction, nucleation, coagulation, condensation, settling and washout. Barrie [6] has presented an improved method of modeling reversible sulphur dioxide exchange between a falling rain drop and air by taking the phenomena associated with ion-enhanced diffusion as well as the microphysical effects of internal circulation. More specific problems dealing with long range transport of airborne materials and/or the effects of deposition, reversible washout have also been discussed, Scriven and Fisher [109, 110], Slinn [117, 118], Smith [120].

It may be noted here that problems such as pollutant dispersion from a time dependent source or effects of foggy environment on dispersion process have not been investigated. Keeping this in view, in Chapter II, the environmental pollution from a time dependent point source with irreversible chemical reaction is studied by using unsteady state three dimensional diffusion equation and in Chapter III, the reversible absorption of a pollutant from an area source in a stagnant fog layer is discussed.

### 1.3 POPULATION DYNAMICS

Population Dynamics deals with the formulation and study of models governing the various types of interactions in biological associations. A successful model is one that explains what is currently happening and predicts what will happen in future. It can be noted that a simple model may not always be realistic and realism might demand more complicated models for biological and ecological systems, though it may be difficult to draw sufficient conclusions from them.

The dynamical system describing the evolution of two interacting species can, in general, be written as

$$\begin{aligned}\frac{dN_1}{dt} &= f(N_1) + \phi(N_1, N_2) \\ \frac{dN_2}{dt} &= g(N_2) + \phi_1(N_1, N_2)\end{aligned}\tag{1.3.1}$$

where  $N_1$  and  $N_2$  represent the population distributions of two species at time  $t$ . Note that the expressions measuring the rate of growth are simply divided into two parts, viz., autogrowth and interaction terms. The terms  $f(N_1)$ ,  $g(N_2)$  stand for the autogrowth of the species and  $\phi(N_1, N_2)$ ,  $\phi_1(N_1, N_2)$  stand for the interactions between the two species. Since  $\phi(N_1, N_2)$  and  $\phi_1(N_1, N_2)$  represent the interactions between the species which affect the rate of growth of each species in different ways, their ratio is a constant (different from unity). If we assume, therefore, that  $\phi_1(N_1, N_2) = \beta \phi(N_1, N_2)$ ,  $\beta$  being a constant, then (1.3.1) becomes

$$\begin{aligned}\frac{dN_1}{dt} &= f(N_1) + \phi(N_1, N_2) \\ \frac{dN_2}{dt} &= g(N_2) + \beta \phi(N_1, N_2).\end{aligned}\tag{1.3.2}$$

The sign of  $f, g, \phi$  and  $\beta$  depend on the mode of interactions between the species. Depending upon various forms of  $\phi$ , (1.3.2) represents different kinds of interactions. The classical Lotka-Volterra equations for system of interacting species is a particular case of the system (1.3.2). Deaklin [23] has established restrictions on the applicability of the conservative Volterra equations in ecological theory. Using Volterra's and other models, Goel et al. [39] have investigated various aspects of the populations of interacting

species exhaustively. Vandermeer and Boucher [129] have analysed the possible types of mutualistic interactions in population models.

Experiments by Holling [57] and a number of other researchers, summarized in Murdoch and Oaten [85], show that the type II response is the most common one and is now widely used in ecological modeling, Evans [31], Hsu [60], Kazarinoff and Driessche [63], Lin and Kahn [73, 74], Oaten and Murdoch [89, 90]. However, it should be noted that functional response of this form has not been considered in the systems of two species with mutualistic or competitive interactions. In this thesis, therefore, we study the following Holling's type of functional response

$$\phi(N_1, N_2) = \frac{\beta' N_1 N_2}{1 + \alpha N_1} \quad (1.3.3)$$

for mutualistic and competitive types of interactions between two species, where  $\alpha$  represents the strength of the functional response and  $\beta'$ , a constant. It is noted that when  $\alpha = 0$ , (1.3.3) corresponds to Volterra's type interaction.

As pointed out earlier, migration of the species plays an important role in the evolution of the species and as such its effects should be taken into account in making the mathematical models by introducing convective and dispersive terms. In contrast to convection, dispersal consists of the



apparently aimless, undirected movements of animals that seem to be wholly random. There is, however, enough evidence in some cases that migration to avoid crowding is the primary cause of dispersal, Gurney and Nisbet [47]. An analytical treatment for the spatial diffusion of a biological population has been given by Skellam [115] in 1951, under the assumption that dispersal is due to random motion of individuals. In this context, a general model has been derived to describe the dynamics of dispersal of biological species whose motion can be viewed as a continuous process, Gurtin and Mac Camy [48], Mc Murtrie [84], Skellam [116]. The effects of convective migration on the species evolution have also been investigated in various cases by making deterministic models, Comins and Blatt [18], Mc Murtrie [84].

Eventhough any realistic model of complex ecosystem is nonlinear and involves many species, mathematical ecologists have largely restricted their nonlinear models to two or three species. In general, the system governing the evolution of the two interacting species with dispersive and convective migration can be written as (Segel and Levin [112], Comins and Blatt [18], Mc Murtrie [84])

$$\begin{aligned} \frac{\partial N_1}{\partial t} + \vec{V}_1 \cdot \Delta N_1 &= f(N_1) + \phi(N_1, N_2) + \Delta \cdot (D_1 \Delta N_1) \\ \frac{\partial N_2}{\partial t} + \vec{V}_2 \cdot \Delta N_2 &= g(N_2) + \beta \phi(N_1, N_2) + \Delta \cdot (D_2 \Delta N_2) \end{aligned} \quad (1.3.4)$$

defined in  $[0, \infty) \times R$ , where  $R$  is a bounded domain with smooth boundary;  $D_1, D_2$  are the positive variable dispersal co-efficients of the species;  $\vec{V}_1, \vec{V}_2$  are convective velocities (constant vectors) of the species.

As investigation of stability of system of the type (1.3.4) in its various forms is going to be an important aspect of our study, in the following, we give an account of the literature related to both the linear and nonlinear stability of such systems.

#### (i) Linear stability

Investigations relating to evolution, linear stability and continued co-existence of interacting species with temporal variations have been quite extensive, Brauer [7], Deaklin [23], Fujii [33], Gilpin [37], Goel et al. [39], Kerner [64], Leou and Tumpson [69], May [81], Maynard Smith [83], Murdoch and Oaten [85], Murray [87], Post and Travis [96], Rescigno and Richardson [101], Travis and Post [128], Vandermeer and Boucher [129]. In particular, Post and Travis [96] have derived sufficient conditions for local stability of interacting communities. Murdoch and Oaten [85] have presented an excellent review of the extensive work on factors that affect the stability of prey-predator interactions, but have limited their discussion to linear stability properties. Gilpin [37] has

investigated the feasibility and stability of prey-predator systems. May [81] has shown that essentially all models that have been proposed for prey-predator systems possess either a stable equilibrium state or a stable limit cycle. Such a stable limit cycle provides a satisfactory explanation for those animal communities in which populations are observed to oscillate in a rather reproducible periodic manner. Leou and Tumpson [69] have established a necessary and sufficient condition for stable co-existence of two species competing for two complementary or substitutable resources. Travis and Post [128] have examined the sensitivity of mutualistic communities to perturbations from the equilibrium and have investigated the response of equilibrium population densities to the changes in environmental and biological parameters.

May [82], in his monograph, has surveyed the work relating to stability versus complexity in mutispecies models. He [79] has proposed a simple mathematical model to caution against the belief that the increase in population stability is a mathematical consequence of the increase in multispecies complexity. He [80] has also discussed the relation between stability and complexity in ecological systems with many interacting species and has shown that complexity decreases the population stability. Steele [123] has considered some ecological models and has pointed out that

complexity can induce stability. By carefully analysing a class of predator-prey models, Gilpin [37] has concluded that ecological systems do persist after enrichment.

Though Skellam [115] has considered the dispersal of the species as early as 1951, extensive investigations relating to the study of effects of migration on the linear stability of the equilibrium state for systems of interacting species are only of recent origin, Casten and Holland [11], Casten and Case [12], Chewing [13], Comins and Blatt [18], Gopalsamy [44, 45], Gurney and Nisbet [47], Haderler et al. [49], Haderler and Rothe [50], Jorne [61], Kerner [65], Levin [70], Murdoch and Oaten [85], Murray [87], Rosen [103], Segel and Jackson [111], Segel and Levin [112], Smith [121], Steele [122]. A more complete review regarding the development of the mathematical theory of spatially distributed populations can be found in Levin [71], McMurtrie [84].

Comins and Blatt [18] have discussed the dynamics of prey-predator association on a spatially nonuniform habitat by means of a biased dispersal and observed that the effect of asymmetry in dispersal is to stabilize the otherwise neutrally stable Lotka-Volterra model. They concluded that the stabilizing effect is not only produced by dispersal but may also be caused by ecological variation. Gurney and Nisbet [47] have shown that dispersal produced by the wholly

random motion is incapable of exerting any stabilizing influence, but an introduction of a suitable nonlinearity into the dispersal behavior of a species whose characteristics are otherwise wholly linear can lead to stabilization under a wide range of conditions. Casten and Case [12] have concluded that the linear stability of the equilibrium state will never be upset after dispersal terms are incorporated into the system for each component species.

Environmental heterogeneity and interacting species systems have also been discussed by various authors, Gopalsamy [45], Levin [71, 72], Maynard Smith [83], Murdoch and Oaten [85], Mc Murtrie [84], Segel and Jackson [111], Steele [122]. Comins and Blatt [18], Levin [70], Murdoch and Oaten [85] and Smith [121] have all studied models of systems showing that the stable co-existence is more probable in a spatially heterogeneous environment than in a homogeneous environment.

Effects of nonhomogeneous boundary conditions on the dynamics of dispersive populations in a linear habitat have also been investigated in cases of competitive and prey-predator systems respectively by Gopalsamy [44] and Haderler et al. [49].

It is noted here that the linear stability of systems such as (1.3.4) with functional response of the form (1.3.3)

has not been investigated and, therefore, we study some problems in this thesis along these lines.

(ii) Nonlinear stability

For nonlinear systems, there is unfortunately no general procedure for obtaining solutions in a closed form. In fact, when a physical problem leads to nonlinear differential equation, one is most often content with qualitative behavior of the solution. It is widely recognized that analysis of nonlinear stability and/or domains of attraction of the equilibrium states is essential for a full understanding of the stability and persistence of ecological systems, a view eloquently expressed by Holling [58]. In such cases, Liapunov's Direct Method is an excellent tool not only to study the nonlinear stability of the equilibrium state for systems of interacting species, but also to investigate the effects of variable dispersal co-efficients on the stability of the equilibrium state generally existing in the real situations. In recent years, various authors have attempted to derive sufficient conditions for nonlinear stability of the equilibrium state for systems of interacting species with temporal variations, Alan Hastings [1], Demetrius [25], Fujii [33], Gatto and Rinaldi [34], Gilpin and Case [38], Goh [40,41,42], Goh and Agnew [43], Harrison [52], Holling [58], Hsu [60], Rosen [104], Siljak [114],

Takeuchi et al. [126]. Fujii [33], in particular, has considered the system with two prey and one predator and has shown that, for a set of parametric values, the three species system can be stable, whereas a system with two prey species without a predator is unstable. He has also shown that his model can have a nonlinearly stable limit cycle in three species even when the equilibrium state is locally unstable. Gatto and Rinaldi [34] have considered a generalized Lotka-Volterra model and have studied the stability properties of its nontrivial equilibrium state by means of an energy function first proposed by Volterra in the context of conservative ecosystems. Hsu [60] has established certain criteria for nonlinear stability of the locally stable equilibrium state. Goh [42] too has investigated the nonlinear stability in a class of prey-predator models including the model in which the predator has type II functional response. Gilpin and Case [38] have demonstrated the existence of multiple domains of attraction in competitive communities. It should be noted that a system with more than one stable equilibrium state could feasibly be driven from one stable state to another by a large perturbation, Holling [58].

Goh [41] has considered the generalized Lotka-Volterra system

$$\frac{dN_i}{dt} = N_i \left( r_i + \sum_{j=1}^n a_{ij} N_j \right), i=1,2,\dots,n \quad (1.3.5)$$

with positive definite function

$$V(N) = \sum_{i=1}^n c_i \left[ N_i - N_i^* - N_i^* \ln \left( \frac{N_i}{N_i^*} \right) \right] \quad (1.3.6)$$

where  $c_1, c_2, \dots, c_n$  are positive constants and  $N_i^*$  ( $i = 1, 2, \dots, n$ ) is the equilibrium state of the system (1.3.5). He has concluded that if the nontrivial equilibrium state of the system (1.3.5) is feasible and if there exists a constant positive diagonal matrix  $C$  with  $c_1, c_2, \dots, c_n$  as diagonal elements such that  $CA + A^T C$  is negative definite, where  $A$  is the matrix formed by interaction co-efficients  $a_{ij}$ , the equilibrium state is nonlinearly stable. When (1.3.5) is considered as a two species system, sufficient conditions for nonlinear stability of the equilibrium state are:

- (i) the equilibrium state is feasible
- (ii) the equilibrium state is locally asymptotically stable
- (iii) both the species sustain density dependent mortalities  
i.e.  $a_{ii} < 0$ ,  $i = 1, 2$ .

Effects of dispersal on the nonlinear stability of the equilibrium state for systems of interacting species have also been studied by various workers, Alan Hastings [2], Chow and Tam [15], Conway and Smoller [19], Harada and Fukao [51], Jorne and Carmi [62], Murray [86], Rosen [102], Rothe [105], Segel and Levin [112], Steele [122]. In particular, Steele [122] has considered a prey-predator



system in a finite one dimensional spatial domain with zero flux boundary conditions and from the analysis, he has conjectured that diffusional effects can never damp out all spatial population fluctuations if the nonlinear terms are included. Murray [86] has demonstrated the error in the above analysis and has shown that the effect of uniform diffusion on the Lotka-Volterra equations for any even number of interacting species is to damp out all spatial variations. However, he has not made any conclusions about the effect of different dispersal abilities of the species. Jorne and Carmi [62] have considered unequal positive dispersal co-efficients in the dispersive Lotka-Volterra system for a number of interacting species with zero flux boundary conditions and have shown that the role of dispersal is to damp out all spatial variations.

Harada and Fukao [51] have investigated the co-existence of two competing species over a linear habitat of finite length by considering the nonlinear effects and have derived approximate conditions for the co-existence of these species using the fundamental mode of spatial variation.

Alan Hastings [2] has further examined the system (1.3.5) with variable dispersal co-efficients i.e. he has considered the system

$$\frac{\partial N_i}{\partial t} = N_i \left( r_i + \sum_{j=1}^n a_{ij} N_j \right) + \sum_{k=1}^m \frac{\partial}{\partial x_k} \left( D_i \frac{\partial N_i}{\partial x_k} \right), \quad i=1,2,\dots,n$$

(1.3.7)

defined in  $[0, \infty) \times R$ , where  $R$  is a bounded domain with smooth boundary and  $D_i (i=1, 2, \dots, n)$  are measures of the dispersal rate which may depend on  $x, t$  or any of the  $N_i$ 's, with boundary conditions

$$\frac{\partial N_i(x, t)}{\partial \hat{n}} = 0 \quad x \in \partial R \quad \text{for } t > 0 \quad (1.3.8) \\ i=1, 2, \dots, n$$

$\hat{n}$  being the unit outward normal vector to the boundary.

Using Liapunov's Direct Method, it has been established that if the equilibrium state is stable without dispersal, it remains so with dispersal.

It should be noted here that in the above studies the nonlinear stability of the dispersive system such as (1.3.7) has only been investigated, but no attempt has been made to investigate such problems with Holling's response which might tend the system towards instability even if it is stable without response.

In this thesis, therefore, the linear and nonlinear stability of the dispersive system of the type (1.3.4) with or without convective migration has been studied by considering Holling's response in linear one, two dimensional and circular habitats using non-homogeneous and homogeneous boundary conditions respectively.

#### 1.4 SPREAD OF GONORRHEA

In general, the spread of communicable epidemic diseases depend upon the number of infectives and susceptibles in the population, modes of communication of the disease, social, cultural and economic conditions of the population, environmental and geographical factors, etc. A detailed account of the study of epidemic diseases can be found in the monographs of Bailey [3,4] and in the lecture notes by Waltman [131]. An interesting review of spread of epidemic diseases has also been presented by Dietz [26]. In particular, spread of infectious disease has been studied by various investigators considering temporal variations, Bailey [3,4], Cooke [20], Hethcote [53, 54], Waltman [131].

Gonorrhea is one of the communicable diseases which spreads by sexual contacts, Bailey [5], Cooke and Yorke [21], Hethcote [55], Lajmanovich and Yorke [66], Wichmann [132]. Cooke and Yorke [21] were the first to develop a mathematical model for gonorrhea. Lajmanovich and Yorke [66] have considered a generalized model for gonorrhea in a nonhomogeneous population and studied asymptotic properties of its equilibrium. Hethcote [55] has used a host-vector model to study the control of gonorrhea. Yorke et al. [133] have pointed out that saturation in a sexually active core population limits the incidence of gonorrhea and

this core causes gonorrhea to remain endemic. Bailey [5] has also reviewed the existing state of development in mathematical modeling of this disease.

In general, the model describing gonorrhea is of host-vector type involving two sets of populations i.e. males and females (Bailey [5], Lajmanovich and Yorke [66], Yorke et al. [133], Wichmann [132]). If  $S_1, N_1$  are number of susceptibles, infectives of male population and  $S_2, N_2$  are the corresponding quantities of female population, then the system describing the temporal variations of the disease when the two populations are mixing homogeneously can be written as (Bailey [5])

$$\begin{aligned} \frac{dS_1}{dt} &= -b_1 S_1 N_2 + a_1 N_1 & \frac{dS_2}{dt} &= -b_2 S_2 N_1 + a_2 N_2 \\ \frac{dN_1}{dt} &= b_1 S_1 N_2 - a_1 N_1 & \frac{dN_2}{dt} &= b_2 S_2 N_1 - a_2 N_2 \end{aligned} \quad (1.4.1)$$

where  $a_1, a_2, b_1, b_2$  are positive constants. In writing (1.4.1), it is assumed that the incubation period (the time elapsing between the receipt of infection and the appearance of symptoms) is assumed to be negligibly small so that an individual becomes infectious to other susceptibles immediately after being infected.

Attempts have also been made to study geographical spread of infectious diseases by considering dispersive migration of susceptibles and infectives, Bailey [3],

Capasso [9], Capasso and Fortunato [10], Marcati and Pozio [77], Radcliffe [97]. In particular, Capasso and Fortunato [10] have studied the asymptotic behavior of a class of reaction diffusion equations related to models for the spatial spread of infectious diseases. Marcati and Pozio [77] have investigated the global behavior of a vector disease model by considering spatial spread and hereditary effects which is applicable to the spread of malaria. They have shown that if the recovery rate is less than or equal to a threshold value, the disease dies out, otherwise the infectious people density tends to a homogeneous distribution. A theoretical expression giving the velocity of propagation for geographical spread of host-vector and carrier borne epidemics have been developed by Radcliffe [97]. Thieme [127] has constructed a deterministic model for the spatial spread of an epidemic.

It may be noted from the above that the effects of dispersal on the spread of gonorrhea has not been investigated. To study such effects, spatial spread of the population must be considered in the mathematical model. In such a case, the equations (1.4.1) governing the population distribution of susceptibles and infectives can be generalized as (Bailey [3,5], Capasso [9], Marcati and Pozio [77], Radcliffe [97])

$$\begin{aligned}
\frac{\partial S_1}{\partial t} &= a_1 N_1 - b_1 S_1 (N_2 + \alpha_1 \frac{\partial^2 N_2}{\partial x^2}) + D_1 \frac{\partial^2 S_1}{\partial x^2} \\
\frac{\partial N_1}{\partial t} &= -a_1 N_1 + b_1 S_1 (N_2 + \alpha_1 \frac{\partial^2 N_2}{\partial x^2}) + D_1 \frac{\partial^2 N_1}{\partial x^2} \\
\frac{\partial S_2}{\partial t} &= a_2 N_2 - b_2 S_2 (N_1 + \alpha_2 \frac{\partial^2 N_1}{\partial x^2}) + D_2 \frac{\partial^2 S_2}{\partial x^2} \\
\frac{\partial N_2}{\partial t} &= -a_2 N_2 + b_2 S_2 (N_1 + \alpha_2 \frac{\partial^2 N_1}{\partial x^2}) + D_2 \frac{\partial^2 N_2}{\partial x^2}
\end{aligned} \tag{1.4.2}$$

where  $D_1, D_2$  are dispersal co-efficients of the male, female populations due to self diffusion; the constants  $\alpha_1, \alpha_2$  are cross dispersal co-efficients of the infectives and  $a_1, a_2, b_1, b_2$  are positive constants.

As the total number of promiscuous males and females are constant

$$\begin{aligned}
\text{i.e. } S_1 + N_1 &= c_1 \\
\text{and } S_2 + N_2 &= c_2
\end{aligned} \tag{1.4.3}$$

the system (1.4.2) can be reduced to the following form

$$\begin{aligned}
\frac{\partial N_1}{\partial t} &= -a_1 N_1 + b_1 (c_1 - N_1) (N_2 + \alpha_1 \frac{\partial^2 N_2}{\partial x^2}) + D_1 \frac{\partial^2 N_1}{\partial x^2} \\
\frac{\partial N_2}{\partial t} &= -a_2 N_2 + b_2 (c_2 - N_2) (N_1 + \alpha_2 \frac{\partial^2 N_1}{\partial x^2}) + D_2 \frac{\partial^2 N_2}{\partial x^2} .
\end{aligned} \tag{1.4.4}$$

In this thesis, the local (linear) and global (nonlinear) stability of the system (1.4.4) is investigated to see the

effects of spatial dispersal on the spread of gonorrhea in Chapter XII.

## 1.5 SUMMARY

In the present chapter, a general introduction for the work presented in the thesis is given.

In Chapter II, the unsteady state problem of pollutant dispersion from a time dependent point source has been investigated by considering the effects of irreversible chemical reaction. In the case of instantaneous point source, it has been shown that the concentration decreases as time increases at a particular location and the point of maximum in the concentration-distance profile moves away from the source as time passes. It has also been shown that the shape of the plume at any instant of time is spherical and its size increases as the diffusion co-efficient increases or chemical reaction rate decreases. However in the case of constant flux, it has been pointed out that the concentration at a particular location increases with time and it decreases as the distance from the source increases at a given instant. In this case, the concentration-distance profile does not have any maximum. It has also been noted that the plume shape is ellipsoid of revolution for large times and its size increases as the diffusion co-efficient increases or chemical reaction rate decreases.

In Chapter III, the reversible absorption of a pollutant from an area source emitting with constant flux in a stagnant fog layer has been discussed. It has been noted that the concentration of the pollutant in the gaseous phase as well as in fog droplets increase with time and decrease as the height from the source increases. It has been further pointed out that the concentration of the pollutant in the gaseous phase increases with the backward reaction rate, but decreases as the forward reaction rate increases. However, reverse is the case for the concentration of the pollutant in fog droplets.

In Chapter IV, effects of convective and dispersive migration on the linear stability of the equilibrium state for two species system with mutualistic interactions and functional response have been investigated. In both finite and semi-infinite habitats, it has been shown that the otherwise stable equilibrium state without dispersal remains so with dispersal under flux and reservoir conditions. It has also been shown that the effects of convective and dispersive migration are to stabilize the equilibrium state further in both one and two dimensional finite habitats under reservoir conditions.

In Chapter V, effects of convective and dispersive migration on the linear stability of prey-predator system with functional response have been studied. In both the cases of finite and infinite habitats, it has been shown that



an otherwise stable equilibrium state without dispersal remains stable with dispersal as well under flux and reservoir conditions. In the case of finite habitat, it has been noted that the instability of the equilibrium state is not affected by dispersal under flux boundary conditions, whereas dispersal can stabilize an otherwise unstable equilibrium state without dispersal under reservoir conditions. Further, under reservoir conditions, it has also been pointed out that the effect of convective migration of the species is not only to stabilize the already stable equilibrium state, but also to stabilize even an otherwise unstable equilibrium state provided a certain condition involving convective and dispersive coefficients holds.

Moreover, it has been pointed out that the equilibrium state which is unstable in one dimensional habitat may become stable in two dimensional finite habitat under reservoir conditions.

In Chapter VI, similar effects have been investigated for a competitive system. Under both flux and reservoir conditions, it has been shown that an otherwise stable equilibrium state without dispersal remains so with dispersal in the case of finite and infinite habitats. However, in the case of finite habitat, dispersal may stabilize even an otherwise unstable equilibrium state under reservoir conditions. Also, the effect of convective migration is to stabilize an otherwise unstable equilibrium state with dispersal.

It has been further pointed out that an unstable equilibrium state in one dimensional habitat may become stable in two dimensional finite habitat under reservoir conditions, as in the case of prey-predator system, provided certain inequality involving convective velocities and dispersal coefficients is satisfied.

In Chapters VII and VIII, studies similar to those in Chapters V and VI have been carried out in circular finite habitats for prey-predator and competitive systems with functional response by considering the effects of dispersal.

In Chapter IX, effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for two species system with mutualistic interactions and functional response have been investigated using Liapunov's Direct Method. It has been found that the equilibrium state is nonlinearly asymptotically stable in the entire positive quadrant of the phase-plane with or without dispersal.

In Chapter X, similar effects on the linear and nonlinear stability of the equilibrium state for prey-predator system with functional response have been studied. The functional response on the equilibrium state has been shown to have a destabilizing effect. It has also been asserted that an otherwise stable equilibrium state without dispersal remains stable with dispersal as well. Further, if the equilibrium state is linearly stable without dispersal, then there exists

a subregion of the positive quadrant in the phase-plane where it is nonlinearly asymptotically stable with or without dispersal.

Various cases under which the equilibrium state is nonlinearly asymptotically stable are discussed and the corresponding regions of stability are also estimated.

By considering the effects of dispersal, the linear and nonlinear stability of the equilibrium state for two competing species system with functional response have been examined in Chapter XI. It has been pointed out that the functional response possesses a destabilizing effect on the equilibrium state. Further, it has been observed that an otherwise stable equilibrium state without dispersal remains so with dispersal.

The regions of attraction in various cases under which the equilibrium state is nonlinearly asymptotically stable have been estimated.

In Chapter XII, effects of dispersal on the linear and nonlinear stability of the endemic equilibrium state for gonorrhea epidemic model have been investigated. It has been noted that the equilibrium state which is nonlinearly stable in the feasible region of the positive quadrant in the phase-plane without dispersal remains so with self dispersal when cross dispersal co-efficients of the infectives are zero. Even in the presence of cross dispersal co-efficients, if the equilibrium state is linearly stable with dispersal (self and cross), there exists a subregion of the feasible region where it is nonlinearly asymptotically stable.

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## CHAPTER II

### ENVIRONMENTAL POLLUTION FROM A TIME DEPENDENT POINT SOURCE

#### 2.1 INTRODUCTION

The dispersion of air pollutant due to point sources has been investigated by several workers using Gaussian plume and other models under various conditions, Gill and Sankar Subramanian [4,5], Hoffert [7], Lamb and Seinfeld [8], Pasquill [9], Pattle [10], Saffman [11], Smith [12,13]. In particular, Lamb and Seinfeld [8] have studied the dispersion of a pollutant from a point source by considering steady state three dimensional diffusion equation with variable diffusivity and wind velocity. Analytical solutions of such equations for an elevated point source have been obtained by Ermak [3] under certain conditions. It may, however, be noted here that the dispersion of pollutants from a point source with time dependent flux has not been studied so far.

Keeping these in view, in this chapter, the pollutant dispersion from a time dependent point source is investigated by considering time dependent three dimensional diffusion equation with first order irreversible chemical reaction.

## 2.2 BASIC EQUATION

Consider the dispersion of a reactive air pollutant from an elevated ( $H$  being the height of the source) point source in a stable environment so that it is reasonable to use the unsteady state convective diffusive equation to describe its concentration distribution. By taking into account the effects of chemical reaction and wind velocity, the equation governing the concentration of the pollutant is written as follows :

$$\frac{\partial c}{\partial t} + V \frac{\partial c}{\partial x} = D \left( \frac{\partial^2 c}{\partial x^2} + \frac{\partial^2 c}{\partial y^2} + \frac{\partial^2 c}{\partial z^2} \right) - kc \quad (2.2.1)$$

where  $V$  (assumed to be a constant) is the mean wind velocity along the horizontal  $x$ -axis,  $D$  is the diffusion coefficient and  $k$  is the rate of chemical reaction.

Taking the source as the origin of the co-ordinate system, the initial and boundary conditions may be written as

$$c(s, 0) = 0 \quad \text{for all } s = (x^2 + y^2 + z^2)^{1/2} > 0$$

$$c(s, t) \rightarrow 0 \quad \text{as } s \rightarrow \infty, \quad \text{for } t \geq 0 \quad (2.2.2)$$

$$-4\pi s^2 D \frac{\partial c}{\partial s} = W(t) \quad \text{as } s \rightarrow 0, \quad \text{for } t \geq 0.$$

The last boundary condition implies that the point source has a prescribed time dependent flux  $W(t)$ . It may be noted that the equations (2.2.1) and (2.2.2) are also applicable

approximately in a nonhomogeneous environment where diffusion co-efficients in the x,y,z directions might slightly vary from each other (see Appendix).

To solve the system (2.2.1) with conditions (2.2.2), taking Laplace transform of (2.2.1) and keeping in view the initial condition, we get

$$V \frac{\partial \bar{c}}{\partial x} = D \left( \frac{\partial^2 \bar{c}}{\partial x^2} + \frac{\partial^2 \bar{c}}{\partial y^2} + \frac{\partial^2 \bar{c}}{\partial z^2} \right) - m \bar{c} \quad (2.2.3)$$

where  $\bar{c}$  is the Laplace transform of  $c$ ,  $m = k+p$  and  $p$  is the Laplace's variable.

The boundary conditions become

$$\bar{c}(s,p) \rightarrow 0 \quad \text{as } s \rightarrow \infty \quad (2.2.4)$$

$$-4\pi s^2 D \frac{\partial \bar{c}}{\partial s} = \bar{W}(p) \quad \text{as } s \rightarrow 0$$

where  $\bar{W}(p)$  is the Laplace transform of  $W(t)$ .

Assuming the solution of (2.2.3) in the form

$$\bar{c} = \exp \left( \frac{Vx}{2D} \right) f(s) \quad (2.2.5)$$

and which on using (2.2.3) and (2.2.4) gives

$$\bar{c} = \frac{\bar{W}(p)}{4\pi D s} \exp \left[ \frac{Vx}{2D} - \left( \frac{V^2}{4D} + \frac{m}{D} \right)^{1/2} s \right]. \quad (2.2.6)$$



By finding inverse Laplace transform of (2.2.6), the solution of (2.2.1) satisfying the initial and boundary conditions is written as

$$c(x,y,z,t) = \frac{1}{4\pi Ds} \left\{ \frac{1}{2\pi i} \int_{\gamma-i\infty}^{\gamma+i\infty} \bar{W}(p) \exp \left[ pt + \frac{Vx}{2D} - \left( \frac{V^2}{4D^2} + \frac{m}{D} \right)^{1/2} s \right] dp \right\} \quad (2.2.7)$$

where  $\gamma$  is a real positive number such that all the singularities lie in the left hand side of the line,  $\text{Re}(p) = \gamma$ , in the Bromwich contour, fig. 2.1.

### 2.3 PARTICULAR CASES

To study the practical situations, various forms of the flux  $W(t)$  have been considered.

#### Case I :

When the point source is instantaneous,  $W(t)$  may be taken as

$$W(t) = W_0 \delta(t)$$

where  $\delta(t)$  is Dirac delta function. This case may be applicable to an instantaneous exhaust of pollutant from a stack or to an explosion of a nuclear device, a gas storage.

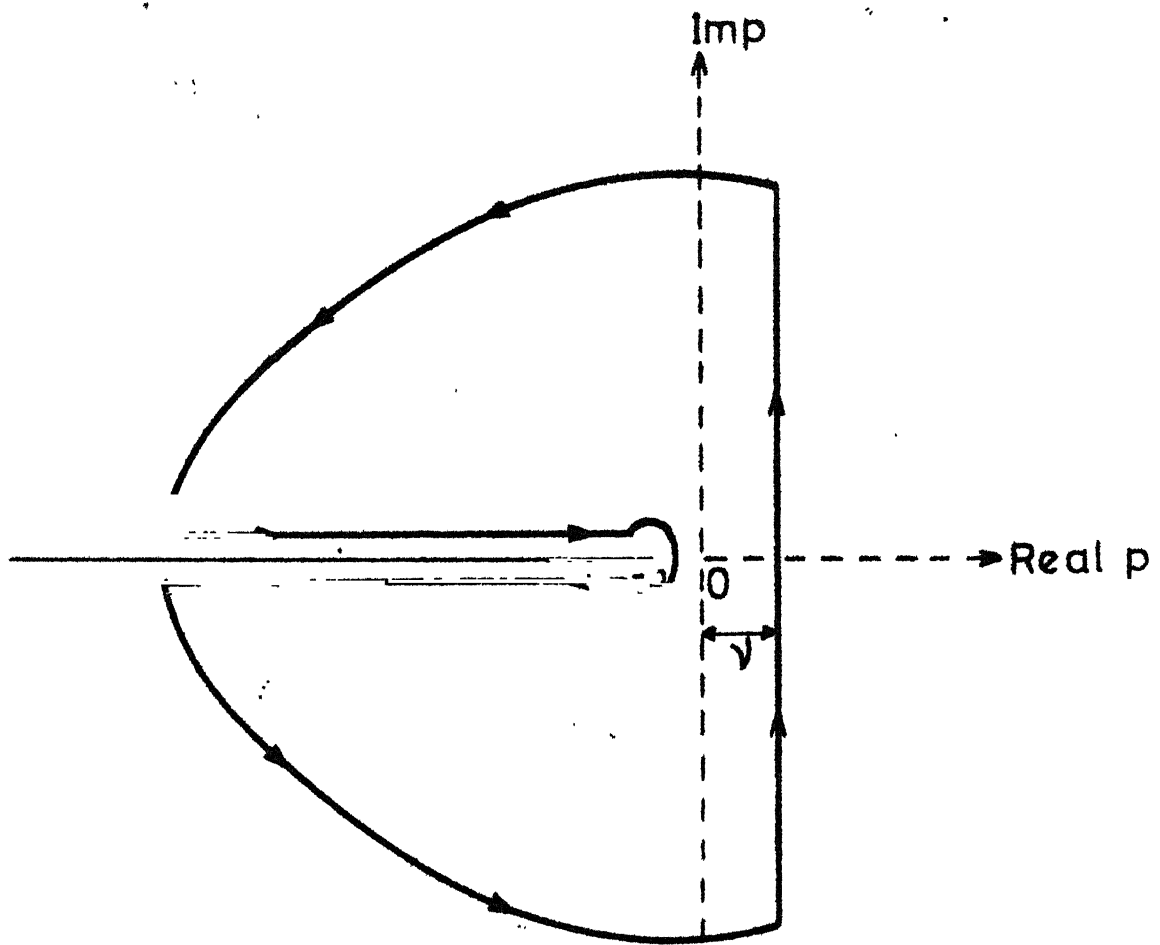


Fig.2.1 Bromwich contour

In this case, using the above expression of  $W(t)$  in (2.2.7), the concentration  $c_1(x,y,z,t)$  can be written as,

$$c_1 = \frac{W_0}{4\pi Ds} \left[ \frac{1}{2\pi i} \int_{\gamma-i\infty}^{\gamma+i\infty} \exp \left\{ pt + \frac{Vx}{2D} - \left( \frac{p+b}{D} \right)^{1/2} s \right\} dp \right] \quad (2.3.1)$$

where

$$b = \frac{V^2}{4D} + k. \quad (2.3.2)$$

The integrand in (2.3.1) has branch point at  $p = -b$ . Using the Bromwich contour of fig. 2.1, this integral can be evaluated to give the concentration distribution as

$$c_1 = \frac{W_0 \exp \left( \frac{Vx}{2D} \right)}{4\pi^2 Ds} \int_b^\infty \exp(-ut) \sin \left[ \left( \frac{u-b}{D} \right)^{1/2} s \right] du. \quad (2.3.3)$$

It may be noted from (2.3.3) that  $c_1$  tends to zero asymptotically as  $t \rightarrow \infty$ .

It is also noted that the expression (2.3.3) can be simplified to the following form

$$c_1 = \frac{W_0}{(4\pi Dt)^{3/2}} \exp \left[ \frac{Vx}{2D} - \left( \frac{V^2}{4D} + k \right) t - \frac{s^2}{4Dt} \right]. \quad (2.3.4)$$

When  $V = 0$ ,  $k = 0$ , it reduces to the same form as given by Carslaw and Jaeger [1].

The shape of the plume at a particular instant of time  $t = t_0$  (say) is obtained by putting  $c_1 = c_0$  (a constant) in (2.3.4), giving

$$\frac{s^2}{4Dt_0} + \left(\frac{V^2}{4D} + k\right) t_0 - \frac{Vx}{2D} = Q_0 \text{ (a constant)}. \quad (2.3.5)$$

Using  $s^2 = x^2 + y^2 + z^2$ , (2.3.5) is written as

$$(x - Vt_0)^2 + y^2 + z^2 = R^2 \quad (2.3.6)$$

where

$$R^2 = 4Dt_0 (Q_0 - kt_0). \quad (2.3.7)$$

It is easily seen that (2.3.6) represents a sphere of radius  $R$  in  $(x, y, z)$  co-ordinates with centre at  $(Vt_0, 0, 0)$  moving with velocity  $V$  along the horizontal  $x$ -axis. It may be noted that the size of the plume increases as  $D$  increases or  $k$  decreases.

Further, the radius of the spherical plume increases as time passes i.e. as  $t_0$  increases till  $t_0 \leq Q_0/2k$  and the rate of increase of this radius increases as  $D$  increases or  $k$ ,  $t_0$  decrease.

The concentration at the ground level can be written, from (2.3.4), as

$$c_1|(x, y, -H, t) = \frac{W_0}{(4\pi Dt)^{3/2}} \exp \left[ -kt - \frac{1}{4Dt} (x-Vt)^2 - \frac{(y^2 + H^2)}{4Dt} \right] \quad (2.3.8)$$

showing that it decreases as the height of the source increases.

The concentration along the central line is also obtained from (2.3.4) by putting  $y = 0$  and  $z = 0$  as

$$c_1|(x,0,0,t) = \frac{W_0}{(4\pi Dt)^{3/2}} \exp \left[ -kt - \frac{1}{4Dt} (x-Vt)^2 \right]. \quad (2.3.9)$$

The expression given by (2.3.9) may be written in the dimensionless form, by using the transformations

$$\begin{aligned} \bar{t} &= \frac{D}{H^2} t, \quad \bar{x} = \frac{x}{H}, \quad \bar{V} = \frac{VH}{D} \\ \bar{k} &= \frac{H^2}{D} k, \quad \bar{b} = \frac{H^2}{D} b, \quad \bar{c}_1 = \frac{H^3}{W_0} c_1 \end{aligned} \quad (2.3.10)$$

and dropping the bars for convenience, as follows

$$c_1|(x,0,0,t) = \frac{1}{(4\pi t)^{3/2}} \exp \left[ -kt - \frac{1}{4t} (x-Vt)^2 \right]. \quad (2.3.11)$$

The expression (2.3.11) for  $c_1|(x,0,0,t)$  is calculated numerically and plotted in fig. 2.2 for different values of  $t$  and  $k = 0.5$ ,  $V = 2.0$ . It is seen from the graph that the concentration decreases as time increases at a particular location and the point of maximum in the concentration-distance profile moves away from the source as time increases.

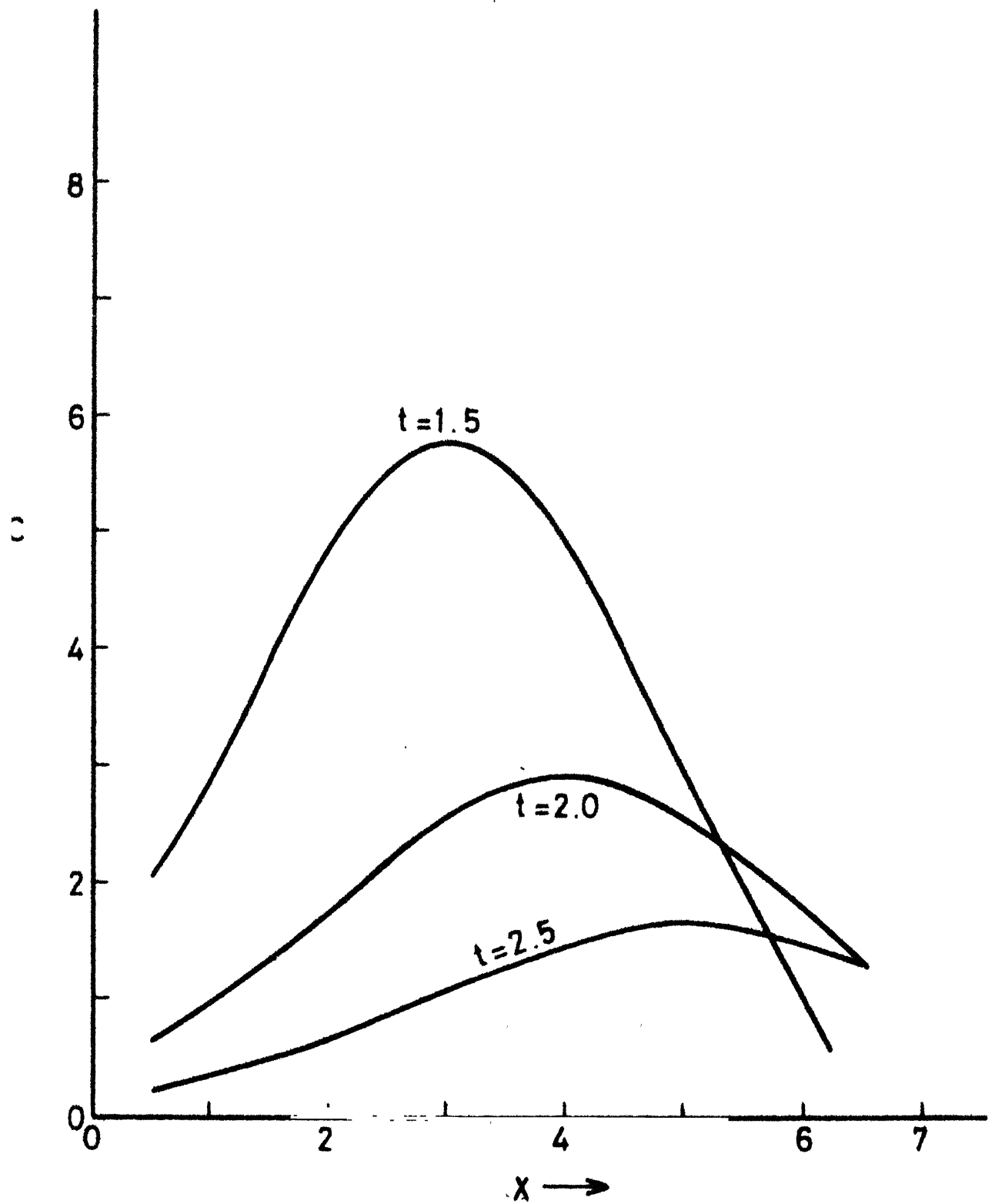


Fig. 2.2 Variation of  $C$  with  $X$  for  $V=2.0$ ,  $k=0.5$

Case II :

When the exhaust (flux) from the point source is uniform

$$\text{i.e. } W(t) = W_1$$

the concentration  $c_2(x,y,z,t)$  of the pollutant can be written, from (2.2.7), as

$$c_2 = \frac{W_1}{4\pi Ds} \exp\left(\frac{Vx}{2D}\right) \frac{1}{2\pi i} \int_{\gamma-i\infty}^{\gamma+i\infty} \frac{1}{p} \exp\left[pt - \left(\frac{p+b}{D}\right)^{1/2} s\right] dp. \quad (2.3.12)$$

In the above expression the integrand has a simple pole at  $p = 0$  and branch point at  $p = -b$ . Using the Bromwich contour of fig. 2.1, this integral can be evaluated as

$$c_2 = \frac{W_1 \exp\left(\frac{Vx}{2D}\right)}{4\pi Ds} \left\{ \exp\left[-\left(\frac{V^2}{4D^2} + \frac{k}{D}\right)^{1/2} s\right] - \frac{1}{\pi} \int_b^\infty \frac{1}{u} \exp(-ut) \sin\left[\left(\frac{u-b}{D}\right)^{1/2} s\right] du \right\}. \quad (2.3.13)$$

The asymptotic form of (2.3.13) may be found by taking the limit as  $t \rightarrow \infty$

$$\text{i.e. } c_2 = \frac{W_1}{4\pi Ds} \exp\left[\frac{Vx}{2D} - \left(\frac{V^2}{4D^2} + \frac{k}{D}\right)^{1/2} s\right]. \quad (2.3.14)$$

It is noted from (2.3.14) that  $c_2$  decreases as  $k$  increases. The expression (2.3.14) is same as the one obtained by Gupta and Gupta [6].

The shape of the plume near the source may be obtained by taking  $c_2 = c_0$  (a constant) in (2.3.14), giving

$$\left(\frac{V^2}{4D^2} + \frac{k}{D}\right)^{1/2} s - \frac{Vx}{2D} = Q_1 \quad (\text{a constant})$$

which on using  $s^2 = x^2 + y^2 + z^2$ , simplifies to

$$k x^2 + \left(\frac{V^2}{4D} + k\right) (y^2 + z^2) - Q_1 Vx = DQ_1^2. \quad (2.3.15)$$

It may be seen that (2.3.15) represents an ellipsoid of revolution in  $(x, y, z)$  system with centre  $\left(\frac{VQ_1}{2k}, 0, 0\right)$  and semi axes  $(A, B, B)$  where

$$\begin{aligned} A^2 &= \frac{Q_1^2}{k} \left[ D + \frac{V^2}{4k} \right] \\ B^2 &= \frac{DQ_1^2}{k}. \end{aligned} \quad (2.3.16)$$

It is observed from (2.3.16) that the size of the plume decreases as  $k$  increases for fixed  $D$ . Further, the size of the ellipsoid increases with  $D$ .

The concentration at the ground level is obtained from (2.3.13) as

$$\begin{aligned} c_2|_{(x,y,-H,t)} &= \frac{W_1 \exp\left(\frac{Vx}{2D}\right)}{4\pi D(x^2 + y^2 + H^2)^{1/2}} \left\{ \exp\left[-\left(\frac{V^2}{4D^2} + \frac{k}{D}\right)^{1/2} \right. \right. \\ &\quad \left. \left. (x^2 + y^2 + H^2)^{1/2} \right] \right. \\ &\quad \left. - \frac{1}{\pi} \int_b^\infty \frac{1}{u} \exp(-ut) \sin\left[\left(\frac{u-b}{D}\right)^{1/2} (x^2 + y^2 + H^2)^{1/2}\right] du \right\}. \end{aligned} \quad (2.3.17)$$



It may be noted from (2.3.17) that the concentration at the ground level decreases as the height of the source increases.

The concentration along the central line can also be obtained from (2.3.13) by putting  $y = 0$  and  $z = 0$  as

$$c_2|_{(x,0,0,t)} = \frac{W_1 \exp\left(\frac{Vx}{2D}\right)}{4\pi Dx} \left\{ \exp\left[-\left(\frac{V^2}{4D} + \frac{k}{D}\right)^{1/2} x\right] - \frac{1}{\pi} \int_b^\infty \frac{1}{u} \exp(-ut) \sin\left[\left(\frac{u-b}{D}\right)^{1/2} x\right] du \right\}. \quad (2.3.18)$$

Using the same dimensionless transformations as in the previous case and defining

$$\bar{c}_2 = \frac{DH}{W_1} c_2 \quad (2.3.19)$$

the expression (2.3.18) is written in the dimensionless form as follows (the bars have been dropped for convenience) :

$$c_2|_{(x,0,0,t)} = \frac{\exp\left(\frac{Vx}{2}\right)}{4\pi x} \left\{ \exp\left[-\left(\frac{V^2}{4} + k\right)^{1/2} x\right] - \frac{1}{\pi} \int_b^\infty \frac{1}{u} \exp(-ut) \sin\left[(u-b)^{1/2} x\right] du \right\}. \quad (2.3.20)$$

The expression (2.3.20) for  $c_2$  is calculated numerically and plotted in fig. 2.3 for different values of  $t$  and  $k = 0.5$ ,  $V = 2.0$ . It is observed from the graph that the concentration of the pollutant at a particular location increases with  $t$

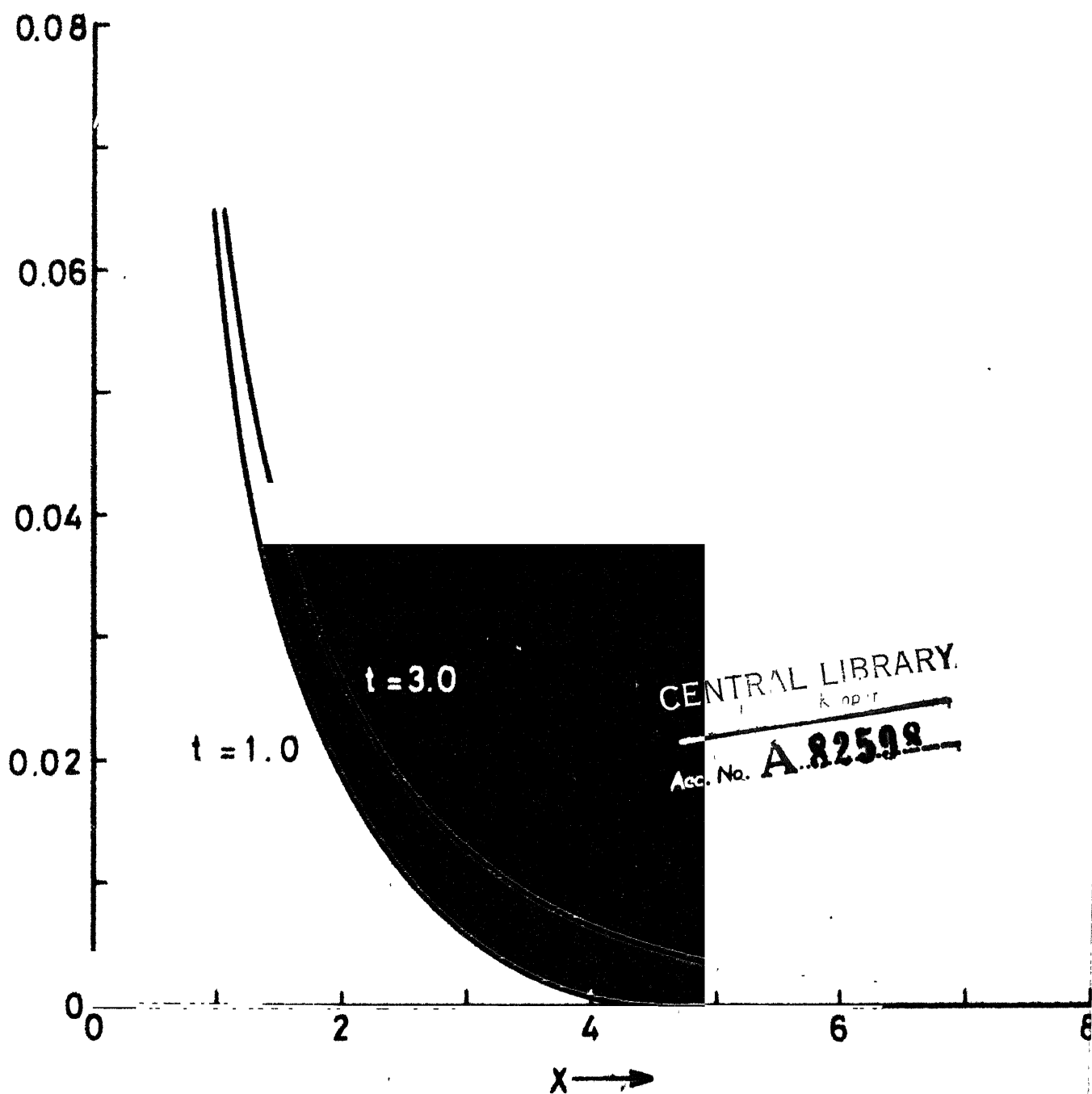


Fig. 2.3 Variation of  $C$  with  $X$  for  $V=2.0$ ,  $k=0.5$

and decreases as  $x$  increases at a given instant. It is also noted that the concentration-distance profile does not have any maximum in this case.

From the above two cases, the following results regarding concentration distribution can also be obtained as shown below :

Case III :  $W(t) = W_1 + W_0 \delta(t - t_0), t \geq 0$

This case corresponds to constant flux for all time  $t$  and an instantaneous flux at time  $t = t_0$ . The concentration  $c_3(x,y,z,t)$  of the pollutant in this case is given by

$$c_3(x,y,z,t) = c_2(x,y,z,t), 0 < t < t_0$$

$$= c_2(x,y,z,t) + c_1(x,y,z,t-t_0), t \geq t_0$$

where  $c_1(x,y,z,t-t_0)$  is obtained from (2.3.4) by replacing  $t$  by  $(t-t_0)$ . When  $t_0 = 0$ , the concentration of the pollutant is given by

$$c_3(x,y,z,t) = c_1(x,y,z,t) + c_2(x,y,z,t).$$

Case IV :  $W(t) = W_0 \delta(t), 0 \leq t < t_0$

$$= W_1, t \geq t_0$$

This case corresponds to an instantaneous flux at time  $t = 0$  and constant flux after an elapse of time  $t_0$ . In this case the concentration  $c_4(x,y,z,t)$  is given by

$$\begin{aligned}
 c_4(x,y,z,t) &= c_1(x,y,z,t) , \quad 0 \leq t < t_0 \\
 &= c_2(x,y,z,t-t_0) + c_1(x,y,z,t) , \quad t \geq t_0
 \end{aligned}$$

where  $c_2(x,y,z,t-t_0)$  is the expression obtained from (2.3.13) by replacing  $t$  with  $(t-t_0)$ .

Case V :  $W(t) = W_0 \delta(t) , \quad 0 \leq t < t_0$

$$= W_0 \delta(t-t_0), t \geq t_0$$

This case corresponds to an instantaneous flux at time  $t = 0$  and another at  $t = t_0$ . In this case concentration  $c_5(x,y,z,t)$  is given by

$$\begin{aligned}
 c_5(x,y,z,t) &= c_1(x,y,z,t) , \quad 0 \leq t < t_0 \\
 &= c_1(x,y,z,t) + c_1(x,y,z,t-t_0) , \quad t \geq t_0 .
 \end{aligned}$$

## 2.4 CONCLUSION

By considering the effects of irreversible chemical reaction, the unsteady state problem of pollutant dispersion from a time dependent point source has been investigated. In the case of instantaneous point source, it has been shown that the concentration decreases as time increases at a particular location and the point of maximum in the concentration-distance profile moves away from the source as time increases. It has also been shown that the shape of the plume at any

instant of time is spherical and its size increases as the diffusion co-efficient increases or chemical reaction rate decreases. However, in the case of constant flux, it has been pointed out that the concentration at a particular location increases with time and it decreases as the distance from the source increases at a given instant. The concentration-distance profile does not have any maximum in this case. It has also been noted that the plume shape in this case is ellipsoid of revolution for large times and its size increases as the diffusion co-efficient increases or chemical reaction rate decreases.

In both the cases, it has also been noticed that the concentration at the ground level decreases as the height of the source increases.

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## APPENDIX

Consider the following partial differential equation,

$$\frac{\partial c}{\partial t} + V \frac{\partial c}{\partial x_1} = D_1 \frac{\partial^2 c}{\partial x_1^2} + D_2 \frac{\partial^2 c}{\partial x_2^2} + D_3 \frac{\partial^2 c}{\partial x_3^2} - kc \quad (i)$$

where  $D_1, D_2, D_3$  are the diffusion coefficients in the directions of  $x_1, x_2$  and  $x_3$  respectively.

The flux  $Q$  at the source may be written as

$$Q = -S.D. \frac{\partial c}{\partial s_1} = W(t), \text{ for } s_1 \rightarrow 0 \quad (ii)$$

where

$$s_1^2 = D_3 \left( \frac{x_1^2}{D_1} + \frac{x_2^2}{D_2} + \frac{x_3^2}{D_3} \right) \quad (iii)$$

represents ellipsoid with semiaxes  $(\sqrt{\frac{D_1}{D_3}} s_1, \sqrt{\frac{D_2}{D_3}} s_1, s_1)$  enclosing the source ( $s_1 \rightarrow 0$ ),  $S$  is the surface area of the ellipsoid and  $D$  is the diffusion co-efficient along the normal to this surface. When  $D_1, D_2, D_3$  are slightly different from each other, the surface area of the ellipsoid can be approximated as

$$\begin{aligned} &= 4\pi \left[ \sqrt{\frac{D_1}{D_3}} s_1 \cdot \sqrt{\frac{D_2}{D_3}} s_1 \cdot s_1 \right]^{2/3} \\ &= 4\pi s_1^2. \end{aligned} \quad (iv)$$

The diffusion co-efficient  $D$  along the normal to the surface having direction cosines  $(l, m, n)$  relative to the

principal axes of diffusion (see [2], p. 7) is given by

$$D = l^2 D_1 + m^2 D_2 + n^2 D_3$$

and hence in the present case

$$D = \frac{\sum \frac{x_1^2}{D_1}}{\sum (\frac{x_1}{D_1})^2} = D_3 . \quad (v)$$

From (ii) to (v), we have

$$- 4\pi s_1^2 D_3 \frac{\partial c}{\partial s_1} = W(t), \text{ when } s_1 \rightarrow 0. \quad (vi)$$

Using the transformations

$$x = (\frac{D_3}{D_1})^{1/2} x_1, y = (\frac{D_3}{D_2})^{1/2} x_2, z = x_3$$

the equation (i) and the condition (vi) reduce to

$$\frac{\partial c}{\partial t} + v \frac{\partial c}{\partial x} = D \left( \frac{\partial^2 c}{\partial x^2} + \frac{\partial^2 c}{\partial y^2} + \frac{\partial^2 c}{\partial z^2} \right) - kc \quad (vii)$$

$$- 4\pi s^2 D \frac{\partial c}{\partial s} = W(t), \text{ for } s \rightarrow 0 \quad (viii)$$

where  $s^2 = x^2 + y^2 + z^2$ .

Remark : It may be noted that a sphere in (x,y,z) system corresponds to an ellipsoid in (x<sub>1</sub>,x<sub>2</sub>,x<sub>3</sub>) system.



## CHAPTER III

### REVERSIBLE ABSORPTION OF A POLLUTANT FROM AN AREA SOURCE IN A STAGNANT FOG LAYER

#### 3.1 INTRODUCTION

The pollutant dispersion from a time dependent point source has been investigated in Chapter II by considering first order irreversible chemical reaction. In the present chapter, the reversible absorption of a pollutant from an area source emitting with constant flux in a stagnant fog layer is discussed.

Various attempts have been made to study the dispersion of the pollutants in the environment from area sources, Draxler [1], Egan and Mahoney [2], Lebedeff and Hameed [3], Liu and Seinfeld [4], Martin [5], Ragland [6], Stern [10]. Specific problems related to deposition and reversible washout have also been studied, Slinn [7,8], Smith [9].

It may be however noted that climatic effects such as presence of fog in the environment on the pollutant dispersion have not been studied. To see such effects in a simplified form, in the following, the pollutant dispersion from an area source in a stagnant fog layer with reversible absorption is studied.

### 3.2 BASIC EQUATIONS

Consider the situation of a stagnant layer of air containing a uniform distribution of fog droplets into which a gaseous pollutant A is emitted at the ground commencing at  $t = 0$ . The pollutant is absorbed reversibly by the droplets according to



where A denotes the species in the gas phase and B is its form dissolved in the droplet phase. The constants  $k_a$  and  $k_b$  are first order forward and backward reaction rates. The gas-phase concentration  $c(z, t)$  in the region  $0 \leq z \leq H$  is given by

$$\frac{\partial c}{\partial t} = K \frac{\partial^2 c}{\partial z^2} - k_a c + k_b c_p \quad (3.2.1)$$

where  $c_p$  denotes the concentration of B,  $K$  is the diffusion co-efficient of the pollutant in the gaseous phase and  $H$  is the thickness of the stagnant fog layer measured vertically from the ground surface  $z = 0$ .

The initial and boundary conditions are written as

$$\begin{aligned} c(z, 0) &= 0 & \text{for } z > 0 \\ -K \frac{\partial c}{\partial z} &= Q & \text{at } z = 0 \\ \frac{\partial c}{\partial z} &= 0 & \text{at } z = H \end{aligned} \quad (3.2.2)$$

As the fog is stationary, the local concentration  $c_p(z, t)$  is described by

$$\frac{\partial c_p}{\partial t} = k_a c - k_b c_p \quad (3.2.3)$$

with initial condition

$$c_p(z, 0) = 0. \quad (3.2.4)$$

Defining the following dimensionless variables

$$\begin{aligned} \bar{c} &= \frac{cK}{QH}, \quad \bar{c}_p = \frac{c_p K}{QH} \\ \tau &= \frac{tK}{H^2}, \quad \eta = \frac{z}{H} \\ \bar{k}_a &= \frac{H^2 k_a}{K}, \quad \bar{k}_b = \frac{H^2 k_b}{K} \end{aligned} \quad (3.2.5)$$

the equations (3.2.1) - (3.2.4) can be written in the dimensionless form as

$$\frac{\partial \bar{c}}{\partial \tau} = \frac{\partial^2 \bar{c}}{\partial \eta^2} - \bar{k}_a \bar{c} + \bar{k}_b \bar{c}_p \quad (3.2.6)$$

with

$$\begin{aligned} \bar{c}(\eta, 0) &= 0 & \eta &> 0 \\ -\frac{\partial \bar{c}}{\partial \eta} &= 1 & \eta &= 0 \\ \frac{\partial \bar{c}}{\partial \eta} &= 0 & \eta &= 1 \end{aligned} \quad (3.2.7)$$

and

$$\frac{\partial \bar{c}_p}{\partial \tau} = \bar{k}_a \bar{c} - \bar{k}_b \bar{c}_p \quad (3.2.8)$$

with

$$\bar{c}_p(n, 0) = 0. \quad (3.2.9)$$

The solution of (3.2.8) subject to (3.2.9) is

$$\bar{c}_p(n, \tau) = \bar{k}_a \int_0^\tau \bar{c}(n, t') \exp [-\bar{k}_b(\tau - t')] dt' \quad (3.2.10)$$

which on substituting in (3.2.6) gives the final equation to govern  $\bar{c}(n, \tau)$  as follows:

$$\frac{\partial \bar{c}}{\partial \tau} = \frac{\partial^2 \bar{c}}{\partial n^2} - \bar{k}_a \bar{c} + \bar{k}_a \bar{k}_b \int_0^\tau \bar{c}(n, t') \exp [-\bar{k}_b(\tau - t')] dt'. \quad (3.2.11)$$

On solving the equation (3.2.11) with conditions (3.2.7) by using Laplace and finite Fourier cosine transforms, we get (dropping the bars for convenience)

$$\begin{aligned} c(n, \tau) = & A_0 + B_0 \exp(-p_{10}\tau) + C_0 \tau \\ & + 2 \sum_{n=1}^{\infty} [A_n + B_n \exp(-p_{1n}\tau) + C_n \exp(-p_{2n}\tau)] \cos(n\pi n) \end{aligned} \quad (3.2.12)$$

and which is used in (3.2.10) to give

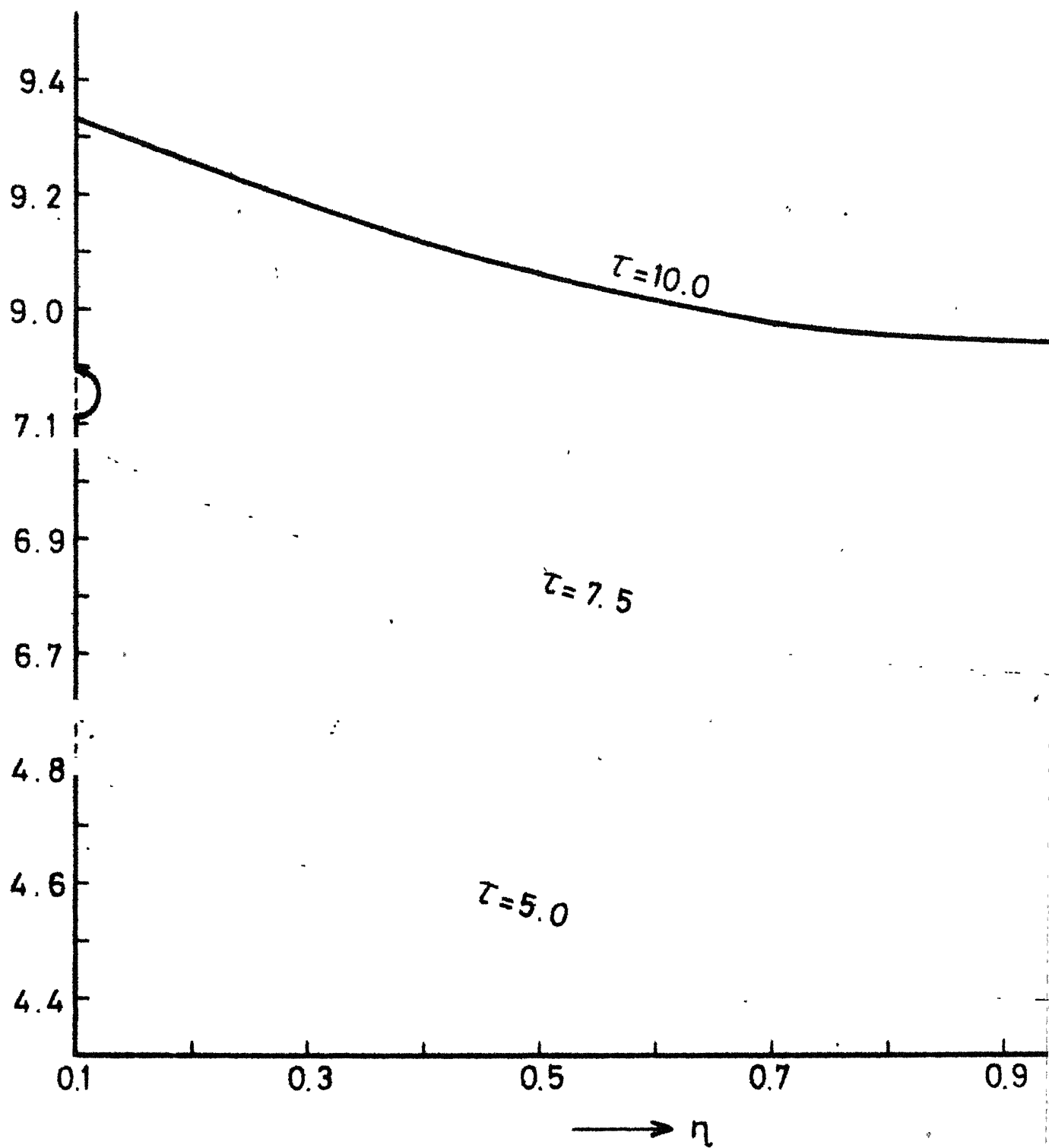


Fig. 3.1 Variation of  $C$  with  $\eta$  for  $k_a = 1.0$ ,  $k_b = 10.0$

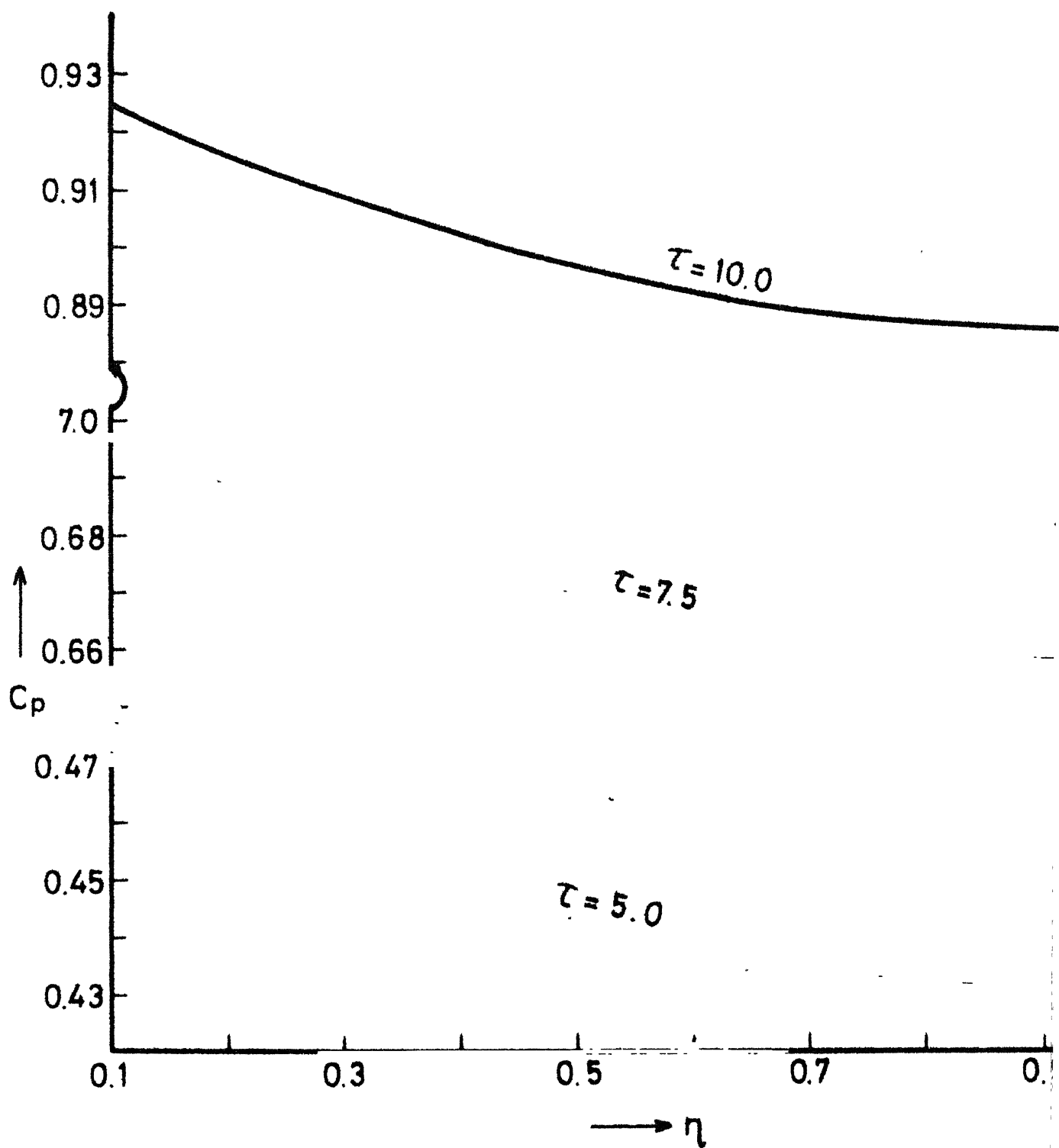


Fig. 3.2 Variation of  $C_p$  with  $\eta$  for  $k_a = 1.0$ ,  $k_b = 10.0$

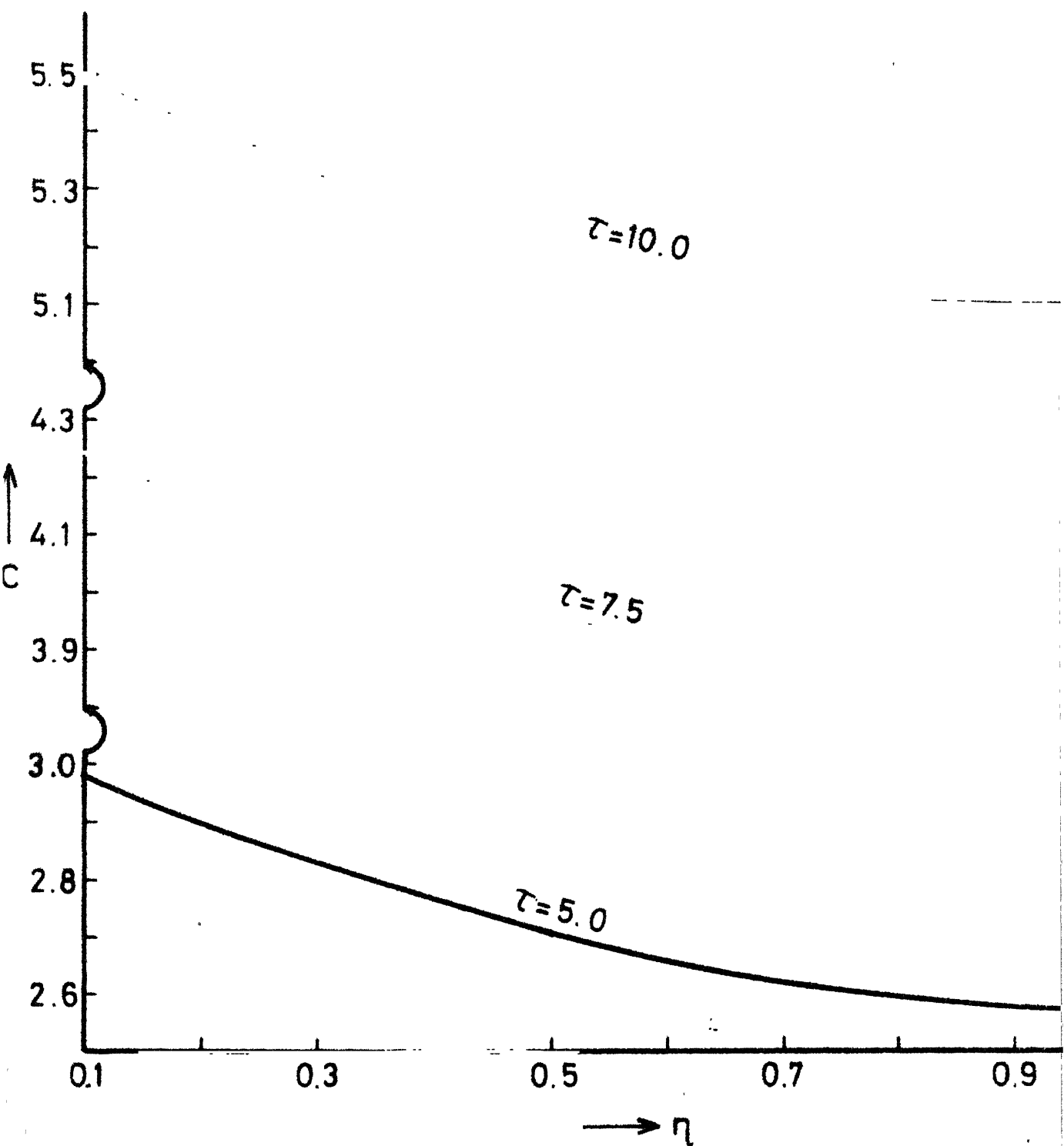


Fig. 3.3 Variation of  $C$  with  $\eta$  for  $k_a = 1.0$ ,  $k_b = 1.0$

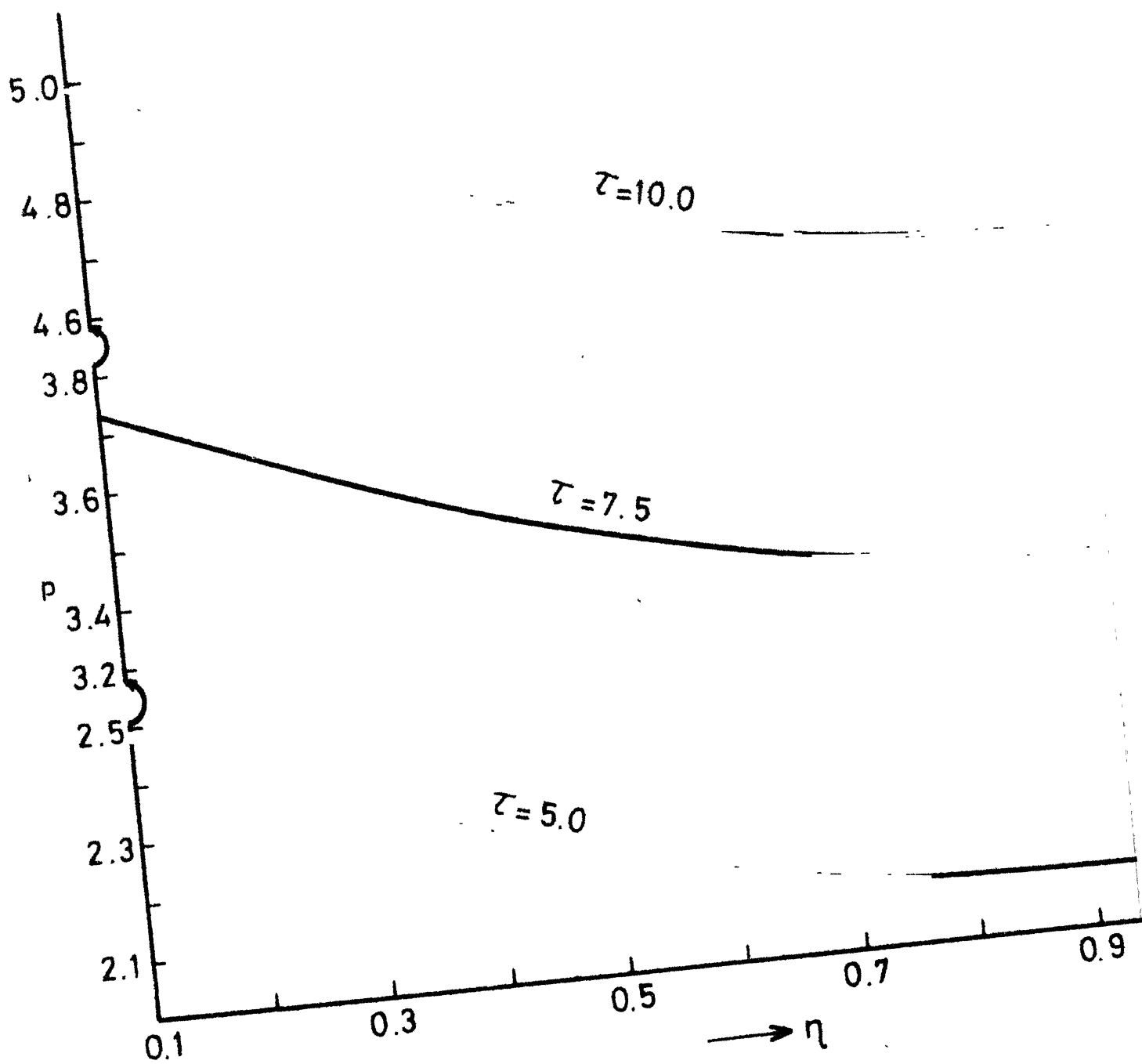


Fig. 3.4 Variation of  $C_p$  with  $\eta$  for  $k_a = 1.0$ ,  $k_b = 1.0$



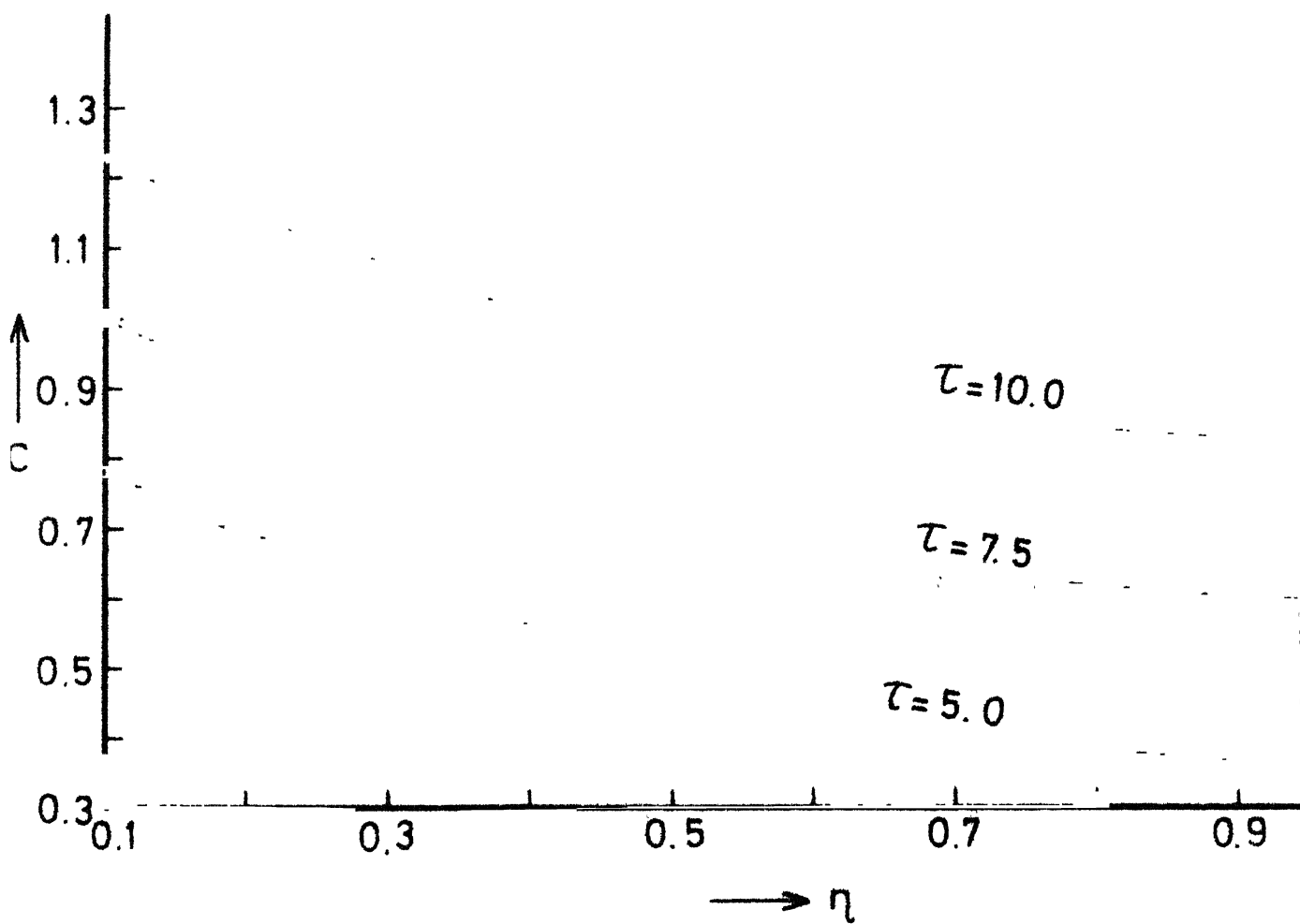


Fig. 3.5 Variation of  $C$  with  $\eta$  for  $k_a = 10.0$ ,  $k_b = 1.0$

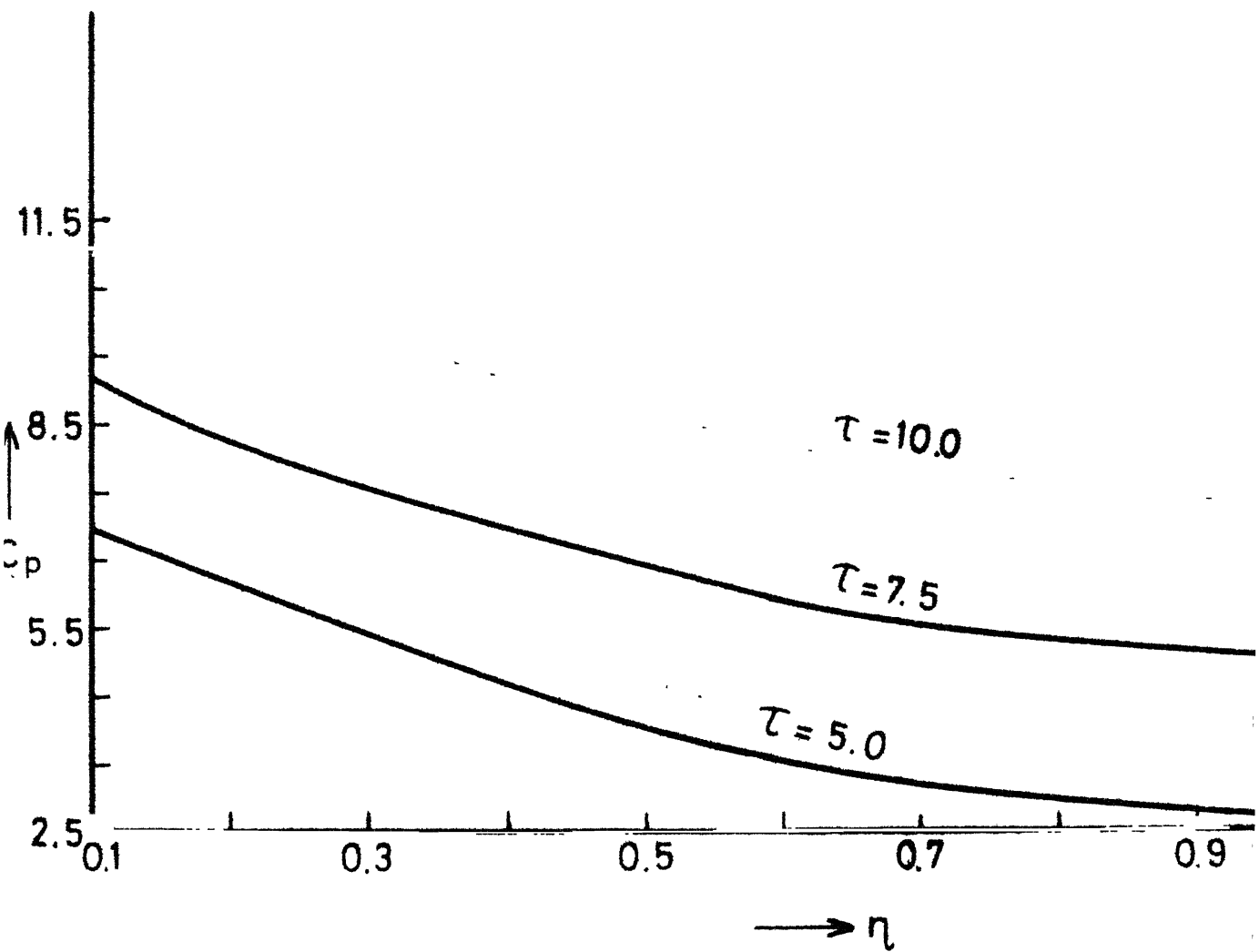


Fig. 3.6 Variation of  $C_p$  with  $\eta$  for  $k_a = 10.0$ ,  $k_b = 1$ .

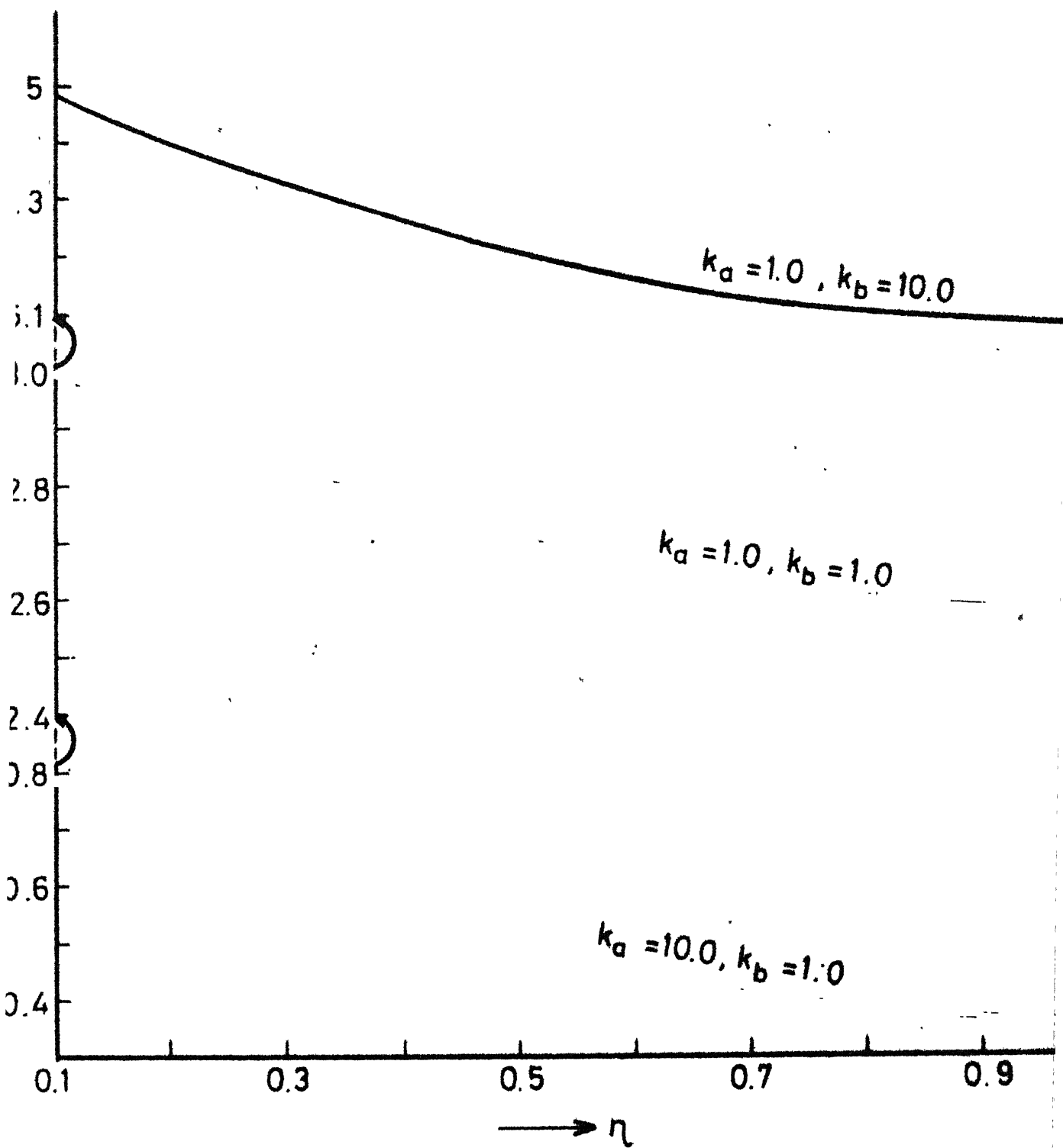
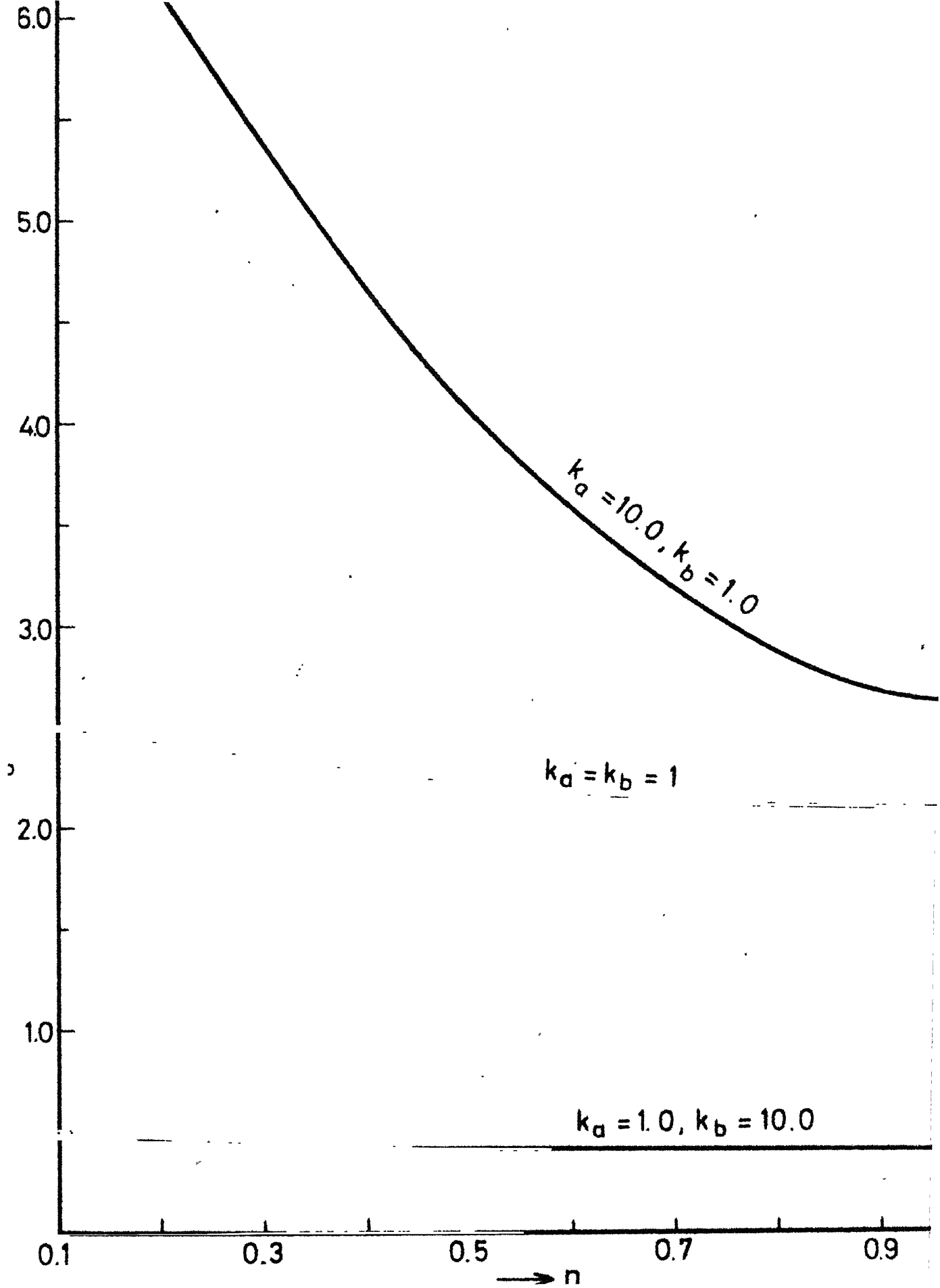


Fig. 3.7 Variation of  $C$  with  $\eta$  for  $\tau = 5.0$



- (i) For fixed  $\tau$ , both  $c$  and  $c_p$  decrease with increasing  $n$ .
- (ii) Both  $c$  and  $c_p$  increase with  $\tau$  at a particular height from the source in the stagnant layer.
- (iii) From fig. 3.1 and 3.2, it can be noted that  $c$  is always greater than  $c_p$  for  $k_a = 1$ ,  $k_b = 10$  at a particular height from the source for all times.
- (iv) For  $k_a = k_b = 1$ , from fig. 3.3 and 3.4, it is also observed that  $c$  is slightly greater than  $c_p$  for all values of  $n$  and  $\tau$  though the values of  $c$  and  $c_p$  are close.
- (v) For all values of  $n$  and  $\tau$ , it is noticed from fig. 3.5 and 3.6 that  $c_p$  is greater than  $c$  for  $k_a = 10$ ,  $k_b = 1$ .
- (vi) At a given height, it is also noted from fig. 3.7 that  $c$  increases with  $k_b$ , but decreases as  $k_a$  increases for fixed  $\tau$ .
- (vii) At a particular height from the source, it may also be seen from fig. 3.8 that  $c_p$  increases with  $k_a$ , but decreases with increasing  $k_b$  for a given instant.

### 3.4 CONCLUSION

The dispersion of a pollutant from an area source emitting with constant flux in a stagnant fog layer has been discussed. It has been shown that both the concentration

of the pollutant in the gaseous phase and fog droplets increase with time and decrease as the height from the source increases. It has also been noted that the concentration of the pollutant in the fog droplets increases and the concentration of the pollutant in the gaseous phase decreases as the forward reaction rate increases, while reverse is the case when the backward reaction rate increases. It has been further seen that the concentration of the pollutant in the gaseous phase is greater or less than the concentration of the pollutant in the fog droplets, at a particular instant and height from the source, depends upon whether the backward reaction rate is greater or less than the forward reaction rate.

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## CHAPTER IV

### EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION ON THE LINEAR STABILITY OF TWO SPECIES SYSTEM WITH MUTUALISTIC INTERACTIONS AND FUNCTIONAL RESPONSE

#### 4.1 INTRODUCTION

In the earlier two chapters, the dispersion of pollutants in air causing the deterioration of the environment and ecology, which might affect the living species in the habitat, has been studied. As pointed out in Section 1.1, such undesirable effects might induce the tendency in the living species to migrate from unfavourable to favourable regions for their survival in the natural habitats. Further, species can also migrate from one region to other due to over crowding, sources of food supply, topographical conditions and environmental and ecological gradients. In general, migration of the species can be studied by identifying it with convective and dispersive processes. Therefore, in Chapters IV to XI, the effects of convective and dispersive migration on the linear and nonlinear stability of systems of interacting species (mutualistic, prey-predator, competitive) living in a linear or circular habitat are studied. In the present chapter, however, we investigate such effects on the mutualistic interactions of two species with functional response.



The evolution and stability of the two interacting species systems with mutualistic interactions (symbiosis) have been studied by various investigators, Cunningham [2], King et al. [6], Rescigno and Richardson [11], Travis and Post [14], Vandermeer and Boucher [15]. In particular, Travis and Post [14] have discussed the response of equilibrium population densities to changes in biological and environmental parameters and concluded that the equilibrium state is stable. It may however be noted here that though the effects of functional response on prey-predator system have been investigated, no attempt has been made to study such effects in the case of symbiosis (Kazarinoff and Driessche [5], Lin and Kahn [8], May [10]). The effects of convective and dispersive migration have also not been discussed on such interactions (Comins and Blatt [1], Haderler et al. [3], Levin [9], Segel and Levin [13]).

Keeping the above in view, in the following, the effects of dispersive migration on the mutualistic interactions of two species system with functional response have been studied in finite and semi-infinite habitats under flux and reservoir boundary conditions. The effect of convective migration on the stability of this system has also been discussed.

Another aim of the chapter is to investigate the premise whether by making a system more complex its stability increases as suggested by Jacquez [4].

## 4.2 BASIC EQUATIONS

Consider the mutualistic interactions of two species in a finite or semi-infinite one dimensional linear habitat. By taking into account the effects of convective and dispersive migration of the species with functional response, the equations governing their evolution can be written as follows (Lin and Kalm [ 8 ], May [ 10 ], Segel and Levin [ 13 ], Travis and Post [ 14 ] ).

$$\frac{\partial N_1}{\partial t} + u_1 \frac{\partial N_1}{\partial x} = a_1 N_1 - a_{11} N_1^2 + a_{12} \frac{N_1 N_2}{1 + \alpha N_1} + D_1 \frac{\partial^2 N_1}{\partial x^2} \quad (4.2.1)$$

$$\frac{\partial N_2}{\partial t} + u_2 \frac{\partial N_2}{\partial x} = a_2 N_2 - a_{22} N_2^2 + a_{21} \frac{N_1 N_2}{1 + \alpha N_1} + D_2 \frac{\partial^2 N_2}{\partial x^2}$$

where  $N_1(x,t)$ ,  $N_2(x,t)$  represent the population distributions of the two species at time  $t$ ;  $D_1, D_2$  their coefficients of dispersal and  $u_1, u_2$  their migration velocities. The interaction coefficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, a_{22}$  and  $\alpha$  are positive constants. The term  $(1 + \alpha N_1)^{-1}$  determines the functional response in the model and the constant  $\alpha$  may be interpreted as the measure of the strength of this response (Kazarinoff and Driessche [ 5 ] ).

Since the trivial equilibrium points are not of much interest in biological systems (Roberts [ 12 ] ), the nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (4.2.1) may be obtained from,

$$a_1 + \frac{a_{12}N_2^*}{1+\alpha N_1^*} = a_{11}N_1^* \quad (4.2.2)$$

$$a_2 + \frac{a_{21}N_1^*}{1+\alpha N_1^*} = a_{22}N_2^* .$$

Eliminating  $N_2^*$  in (4.2.2), we get the cubic equation for  $N_1^*$  as

$$N_1^{*3} + \left( \frac{2}{\alpha} - \frac{a_1}{a_{11}} \right) N_1^{*2} + \frac{1}{a_{11}a_{22}\alpha^2} [a_{11}a_{22} - a_{12}a_{21} - \alpha(a_2a_{12} + 2a_1a_{22})] N_1^* - \frac{a_2a_{12} + a_1a_{22}}{a_{11}a_{22}\alpha^2} = 0 . \quad (4.2.3)$$

After examining the nature of the coefficients of  $N_1^*$  in (4.2.3), it is seen that there exists only one positive value for  $N_1^*$  and therefore for  $N_2^*$ .

However, for  $\alpha=0$ , solving (4.2.2) we get the following positive equilibrium point

$$N_1^* = \frac{a_2a_{12} + a_1a_{22}}{a_{11}a_{22} - a_{12}a_{21}}; \quad N_2^* = \frac{a_1a_{21} + a_2a_{11}}{a_{11}a_{22} - a_{12}a_{21}} \quad (4.2.4)$$

provided

$$a_{11}a_{22} > a_{12}a_{21} \quad (4.2.5)$$

which implies that intraspecific interactions are more stronger than interspecific interactions.

To investigate the local stability of the equilibrium state  $(N_1^*, N_2^*)$  for  $\alpha \geq 0$ , we linearise the system (4.2.1) by writing

$$\begin{aligned} N_1(x,t) &= N_1^* + u(x,t) \\ N_2(x,t) &= N_2^* + v(x,t) . \end{aligned} \quad (4.2.6)$$

On substituting (4.2.6) in the system (4.2.1) and using (4.2.2), we get the following equations

$$\begin{aligned} \frac{\partial u}{\partial t} + u_1 \frac{\partial u}{\partial x} &= -eu + fv + D_1 \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} + u_2 \frac{\partial v}{\partial x} &= gu - hv + D_2 \frac{\partial^2 v}{\partial x^2} \end{aligned} \quad (4.2.7)$$

where  $e, f, g, h$  are positive constants given by,

$$\begin{aligned} e &= N_1^* \left[ a_{11} + \frac{\alpha a_{12} N_2^*}{(1 + \alpha N_1^*)^2} \right]; \quad f = \frac{a_{12} N_1^*}{(1 + \alpha N_1^*)} \\ g &= \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2}; \quad h = a_{22} N_2^* \end{aligned} \quad (4.2.8a)$$

and

$$eh > fg \quad (4.2.8b)$$

for  $\alpha \geq 0$ .

In absence of convective and dispersive migration, it can be easily seen from (4.2.7) that the positive equilibrium state  $(N_1^*, N_2^*)$  is stable for  $\alpha \geq 0$ .

To investigate the stability of the equilibrium state for  $\alpha \geq 0$ , the system (4.2.7) may be associated with the following conditions:

(i) Flux conditions

$$\begin{aligned} u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\ -D_1 \frac{\partial u(0,t)}{\partial x} &= U, \quad -D_2 \frac{\partial v}{\partial x}(0,t) = V & t \geq 0 \\ \frac{\partial u(x,t)}{\partial x} &\rightarrow 0, \quad \frac{\partial v(x,t)}{\partial x} \rightarrow 0 \end{aligned} \quad (4.2.9)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

(ii) Reservoir conditions

$$\begin{aligned} u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\ u(0,t) &= U_1, \quad v(0,t) = V_1 & t \geq 0 \\ u(x,t) &\rightarrow 0, \quad v(x,t) \rightarrow 0 \end{aligned} \quad (4.2.10)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

### 4.3 STABILITY ANALYSIS WITH DISPERSAL IN A FINITE HABITAT

In the following, we study the stability of the equilibrium state with dispersal in a finite habitat when flux or reservoir boundary conditions are prescribed ( $\mu_1 = \mu_2 = 0$ ).

Case (i) Flux conditions

In this case, on solving the system (4.2.7) for  $\mu_1 = \mu_2 = 0$  with flux conditions (4.2.9) by using Laplace

and finite Fourier cosine transforms, we obtain  $u(x, t)$  and  $v(x, t)$  as

$$\begin{aligned}
 u(x, t) = & \frac{1}{L} \int_0^t [A_0 \exp(-p_{10}T) + B_0 \exp(-p_{20}T)] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t [A_n \exp(-p_{1n}T) + B_n \exp(-p_{2n}T)] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} [F_{10} \exp(-p_{10}t) + F_{20} \exp(-p_{20}t)] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \{F_{1n} \exp(-p_{1n}t) + F_{2n} \exp(-p_{2n}t)\} \cos \frac{n\pi x}{L}
 \end{aligned} \tag{4.3.1}$$

$$\begin{aligned}
 v(x, t) = & \frac{1}{L} \int_0^t [C_0 \exp(-p_{10}T) + E_0 \exp(-p_{20}T)] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t [C_n \exp(-p_{1n}T) + E_n \exp(-p_{2n}T)] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} [G_{10} \exp(-p_{10}t) + G_{20} \exp(-p_{20}t)] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \{G_{1n} \exp(-p_{1n}t) + G_{2n} \exp(-p_{2n}t)\} \cos \frac{n\pi x}{L}
 \end{aligned} \tag{4.3.2}$$

where

$$A_n = \frac{(p_{1n} - h - \frac{n^2 \pi^2}{L^2} D_2) U - fV}{p_{1n} - p_{2n}}$$

$$B_n = \frac{(\frac{n^2 \pi^2}{L^2} D_2 + h - p_{2n}) U + fV}{p_{1n} - p_{2n}}$$

$$C_n = \frac{(p_{1n} - e - \frac{n^2 \pi^2}{L^2} D_1) V - gU}{p_{1n} - p_{2n}}$$

$$E_n = \frac{(\frac{n^2 \pi^2}{L^2} D_1 + e - p_{2n}) V + gU}{p_{1n} - p_{2n}} \quad (4.3.3)$$

$$F_{1n} = \frac{(p_{1n} - h - \frac{n^2 \pi^2}{L^2} D_2) R_n - fS_n}{p_{1n} - p_{2n}}$$

$$F_{2n} = \frac{(\frac{n^2 \pi^2}{L^2} D_2 + h - p_{2n}) R_n + fS_n}{p_{1n} - p_{2n}}$$

$$G_{1n} = \frac{(p_{1n} - e - \frac{n^2 \pi^2}{L^2} D_1) S_n - gR_n}{p_{1n} - p_{2n}}$$

$$G_{2n} = \frac{(\frac{n^2 \pi^2}{L^2} D_1 + e - p_{2n}) S_n + gR_n}{p_{1n} - p_{2n}} \quad (4.3.4)$$

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} \left( \frac{n^2 \pi^2}{L^2} D_1 + \frac{n^2 \pi^2}{L^2} D_2 + e + h \right) \pm \frac{1}{2} \left[ \left( \frac{n^2 \pi^2}{L^2} D_1 - \frac{n^2 \pi^2}{L^2} D_2 + e - h \right)^2 + 4fg \right]^{1/2} \quad (4.3.5)$$

and  $(\quad)_0, (\quad)_{10}, (\quad)_{20}$  can be obtained from the corresponding expressions of  $(\quad)_n, (\quad)_{1n}, (\quad)_{2n}$  by putting  $n = 0$ . The constants  $R_n, S_n$  are given by

$$R_n = \int_0^L r(x) \cos \frac{n\pi x}{L} dx$$

$$S_n = \int_0^L s(x) \cos \frac{n\pi x}{L} dx.$$

Since  $p_{1n}, p_{2n}(n=1,2,3,\dots)$  are positive and increase with dispersal co-efficients (see appendix), the nonstationary solutions(4.3.1) and (4.3.2) converge to the following forms as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(x,t) = \frac{1}{L} \left[ \frac{A_0}{p_{10}} + \frac{B_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{A_n}{p_{1n}} + \frac{B_n}{p_{2n}} \right] \cos \frac{n\pi x}{L} \quad (4.3.6)$$

$$\lim_{t \rightarrow \infty} v(x,t) = \frac{1}{L} \left[ \frac{C_0}{p_{10}} + \frac{E_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{C_n}{p_{1n}} + \frac{E_n}{p_{2n}} \right] \cos \frac{n\pi x}{L} \quad (4.3.7)$$

and the rate of convergence increases with dispersal co-efficients. Further, as (4.3.6) and (4.3.7) satisfy the steady state form of the system (4.2.7) with boundary conditions (4.2.9), the equilibrium state is asymptotically stable for  $\alpha \geq 0$  and the degree of stability (i.e. the rate of convergence of nonstationary solutions to stationary solutions) increases as dispersal co-efficients increase.



## Case (ii) Reservoir Conditions

On solving the system (4.2.7) for  $u_1 = u_2 = 0$  with conditions (4.2.1C) by using Laplace and finite Fourier sine transforms, we get  $u(x, t)$  and  $v(x, t)$  as

$$\begin{aligned}
 u(x, t) = & \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left\{ \int_0^t \left[ A'_n \exp(-p_{1n}T) \right. \right. \\
 & \left. \left. + B'_n \exp(-p_{2n}T) \right] dT \right\} \sin \frac{n\pi x}{L} \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ F'_{1n} \exp(-p_{1n}t) + F'_{2n} \exp(-p_{2n}t) \right] \sin \frac{n\pi x}{L}
 \end{aligned} \tag{4.3.8}$$

$$\begin{aligned}
 v(x, t) = & \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left\{ \int_0^t \left[ C'_n \exp(-p_{1n}T) \right. \right. \\
 & \left. \left. + E'_n \exp(-p_{2n}T) \right] dT \right\} \sin \frac{n\pi x}{L} \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ G'_{1n} \exp(-p_{1n}t) + G'_{2n} \exp(-p_{2n}t) \right] \sin \frac{n\pi x}{L}
 \end{aligned} \tag{4.3.9}$$

where

$$\begin{aligned}
 A'_n &= \frac{(p_{1n} - \frac{n^2\pi^2}{L^2} D_2 - h) D_1 U_1 - f D_2 V_1}{p_{1n} - p_{2n}} \\
 B'_n &= \frac{(\frac{n^2\pi^2}{L^2} D_2 + h - p_{2n}) D_1 U_1 + f D_2 V_1}{p_{1n} - p_{2n}} \\
 C'_n &= \frac{(p_{1n} - \frac{n^2\pi^2}{L^2} D_1 - e) D_2 V_1 - g D_1 U_1}{p_{1n} - p_{2n}} \\
 E'_n &= \frac{(\frac{n^2\pi^2}{L^2} D_1 + e - p_{2n}) D_2 V_1 + g D_1 U_1}{p_{1n} - p_{2n}}
 \end{aligned} \tag{4.3.10}$$

$$\begin{aligned}
F'_{1n} &= \frac{(p_{1n} - \frac{n^2 \pi^2}{L^2} D_2 - h) R'_n - f S'_n}{p_{1n} - p_{2n}} \\
F'_{2n} &= \frac{(\frac{n^2 \pi^2}{L^2} D_2 + h - p_{2n}) R'_n + f S'_n}{p_{1n} - p_{2n}} \\
G'_{1n} &= \frac{(p_{1n} - \frac{n^2 \pi^2}{L^2} D_1 - e) S'_n - g R'_n}{p_{1n} - p_{2n}} \\
G'_{2n} &= \frac{(\frac{n^2 \pi^2}{L^2} D_1 + e - p_{2n}) S'_n + g R'_n}{p_{1n} - p_{2n}}
\end{aligned} \tag{4.3.11}$$

$p_{1n}, p_{2n}$  are defined in (4.3.5) and  $R'_n, S'_n$  are given by

$$\begin{aligned}
R'_n &= \int_0^L r(x) \sin \frac{n\pi x}{L} dx \\
S'_n &= \int_0^L s(x) \sin \frac{n\pi x}{L} dx .
\end{aligned}$$

Since  $p_{1n}, p_{2n}$  ( $n=1, 2, 3, \dots$ ) are positive, the nonstationary solutions (4.3.8) and (4.3.9) converge to the following forms as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(x, t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{A'_n}{p_{1n}} + \frac{B'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L} \tag{4.3.12}$$

$$\lim_{t \rightarrow \infty} v(x, t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{C'_n}{p_{1n}} + \frac{E'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L} \tag{4.3.13}$$

and the rate of convergence increases with dispersal co-efficients. As (4.3.12) and (4.3.13) satisfy the steady state form of the system (4.2.7) with boundary conditions (4.2.10), the equilibrium state is asymptotically stable for  $\alpha \geq 0$  and the degree of stability increases with dispersal co-efficients under reservoir conditions also.

#### 4.4 STABILITY ANALYSIS WITH DISPERSAL IN AN INFINITE HABITAT

In the following, the stability analysis of the equilibrium state without convection ( $u_1 = u_2 = 0$ ) is discussed in a semi-infinite habitat under flux and reservoir conditions (4.2.9), (4.2.10) respectively.

##### Case (i) Flux Conditions

In this case, on solving the system (4.2.7) for  $u_1 = u_2 = 0$  with conditions (4.2.9), we obtain

$$\begin{aligned} \bar{u}(x,p) = & \frac{1}{D_1 D_2 p} \left\{ \frac{A(p)}{y_1^{1/2}(p)} \exp [-y_1^{1/2}(p)x] \right. \\ & + \frac{B(p)}{y_2^{1/2}(p)} \exp [-y_2^{1/2}(p)x] \Big\} \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp [-y_1^{1/2}(p)z]}{y_1^{1/2}(p)} [F_1(p, z+x) \right. \\ & + F_1(p, |z-x|)] + \frac{\exp [-y_2^{1/2}(p)z]}{y_2^{1/2}(p)} \\ & \left. [F_2(p, z+x) + F_2(p, |z-x|)] \right\} dz \end{aligned} \quad (4.4.1)$$

$$\begin{aligned}
\bar{v}(x,p) = & \frac{1}{D_1 D_2 p} \left\{ \frac{C(p)}{y_1^{1/2}(p)} \exp \left[ -y_1^{1/2}(p)x \right] \right. \\
& + \frac{E(p)}{y_2^{1/2}(p)} \exp \left[ -y_2^{1/2}(p)x \right] \left. \right\} \\
& + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp \left[ -y_1^{1/2}(p)z \right]}{y_1^{1/2}(p)} \left[ G_1(p, z+x) \right. \right. \\
& + \left. \left. G_1(p, |z-x|) \right] + \frac{\exp \left[ -y_2^{1/2}(p)z \right]}{y_2^{1/2}(p)} \right. \\
& \left. \left[ G_2(p, z+x) + G_2(p, |z-x|) \right] \right\} dz
\end{aligned} \tag{4.4.2}$$

where  $\bar{u}(x,p)$ ,  $\bar{v}(x,p)$  are Laplace transforms of  $u(x,t)$ ,  $v(x,t)$  respectively and

$$A(p) = \frac{(D_2 y_1 - p - h) U - fV}{y_1 - y_2} ; B(p) = \frac{(p + h - D_2 y_2) U + fV}{y_1 - y_2} \tag{4.4.3}$$

$$C(p) = \frac{(D_1 y_1 - p - e) V - gU}{y_1 - y_2} ; E(p) = \frac{(p + e - D_1 y_2) V + gU}{y_1 - y_2}$$

$$F_1(p, x) = \frac{(D_2 y_1 - p - h) r(x) - f s(x)}{y_1 - y_2}$$

$$F_2(p, x) = \frac{(p + h - D_2 y_2) r(x) + f s(x)}{y_1 - y_2}$$

$$G_1(p, x) = \frac{(D_1 y_1 - p - e) s(x) - g r(x)}{y_1 - y_2}$$

$$G_2(p, x) = \frac{(p + e - D_1 y_2) s(x) + g r(x)}{y_1 - y_2} \tag{4.4.4}$$

$$\begin{pmatrix} y_1(p) \\ y_2(p) \end{pmatrix} = \frac{1}{2} \left( \frac{p+e}{D_1} + \frac{p+h}{D_2} \right) \pm \frac{1}{2} \left[ \left( \frac{p+e}{D_1} - \frac{p+h}{D_2} \right)^2 + \frac{4fg}{D_1 D_2} \right]^{1/2}. \quad (4.4.5)$$

Since  $eh > fg$ , it may be noted from (4.4.5) that  $y_1$  and  $y_2$  are positive for all values of  $p \geq 0$  and this fact is used in obtaining the solutions (4.4.1) and (4.4.2).

To investigate the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$  as  $t \rightarrow \infty$ , we use the following property of Laplace transform (see [7], p. 315)

$$\lim_{t \rightarrow \infty} u(x,t) = \lim_{p \rightarrow 0} p \bar{u}(x,p). \quad (4.4.6)$$

Using (4.4.6) in (4.4.1) and (4.4.2), we get

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{A(0)}{y_1^{1/2}(0)} \exp \left[ -y_1^{1/2}(0)x \right] \right. \\ \left. + \frac{B(0)}{y_2^{1/2}(0)} \exp \left[ -y_2^{1/2}(0)x \right] \right\} \quad (4.4.7) \end{aligned}$$

$$\begin{aligned} \lim_{t \rightarrow \infty} v(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{C(0)}{y_1^{1/2}(0)} \exp \left[ -y_1^{1/2}(0)x \right] \right. \\ \left. + \frac{E(0)}{y_2^{1/2}(0)} \exp \left[ -y_2^{1/2}(0)x \right] \right\} \quad (4.4.8) \end{aligned}$$

where  $y_1(0)$ ,  $y_2(0)$  are values of  $y_1(p)$ ,  $y_2(p)$  for  $p=0$  respectively and  $A(0)$ ,  $B(0)$ ,  $C(0)$ ,  $E(0)$  are obtained by putting  $p=0$  in the corresponding expressions (4.4.3).

It can be verified that the expressions (4.4.7) and (4.4.8) satisfy the steady state form of the system (4.2.7), (4.2.9). Thus it may be noted that the nonstationary solutions tend to the corresponding stationary solutions when  $t \rightarrow \infty$ , showing the asymptotic stability of the equilibrium state under flux boundary conditions.

#### Case (ii) Reservoir conditions

As before, on solving the system (4.2.7) for  $u_1 = u_2 = 0$  with conditions (4.2.10), we obtain

$$\begin{aligned} \bar{u}(x,p) = & \frac{1}{D_1 D_2 p} \{ A'(p) \exp [-y_1^{1/2}(p) \bar{x}] \\ & + B'(p) \exp [-y_2^{1/2}(p) \bar{x}] \} \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp [-y_1^{1/2}(p) z]}{y_1^{1/2}(p)} \right. \\ & \quad \left. [F_1(p, z+x) - F_1(p, z-x)] \right. \\ & \quad \left. + \frac{\exp [-y_2^{1/2}(p) z]}{y_2^{1/2}(p)} [F_2(p, z+x) - F_2(p, z-x)] \right\} dz \end{aligned} \quad (4.4.9)$$

$$\begin{aligned}
\bar{v}(x,p) = & \frac{1}{D_1 D_2 p} \{ C'(p) \exp [-y_1^{1/2}(p)x] \\
& + E'(p) \exp [-y_2^{1/2}(p)x] \} \\
& + \frac{1}{2D_1 D_2} \int_0^\infty \{ \frac{\exp [-y_1^{1/2}(p)z]}{y_1^{1/2}(p)} \\
& [G_1(p, z+x) - G_1(p, z-x)] + \frac{\exp [-y_2^{1/2}(p)z]}{y_2^{1/2}(p)} \\
& [G_2(p, z+x) - G_2(p, z-x)] \} dz
\end{aligned} \tag{4.4.10}$$

where  $\bar{u}(x,p)$ ,  $\bar{v}(x,p)$  are Laplace transforms of  $u(x,t)$ ,  $v(x,t)$  respectively and

$$\begin{aligned}
A'(p) &= \frac{(D_2 y_1 - p - h) D_1 U_1 - f D_2 V_1}{y_1 - y_2} \\
B'(p) &= \frac{(p + h - D_2 y_2) D_1 U_1 + f D_2 V_1}{y_1 - y_2} \\
C'(p) &= \frac{(D_1 y_1 - p - e) D_2 V_1 - g D_1 U_1}{y_1 - y_2} \\
E'(p) &= \frac{(p + e - D_1 y_2) D_2 V_1 + g D_1 U_1}{y_1 - y_2} .
\end{aligned} \tag{4.4.11}$$

To investigate the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$  as  $t \rightarrow \infty$ , we use the property of Laplace transform given by (4.4.6) in (4.4.9) and (4.4.10) to get

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x,t) = \frac{1}{D_1 D_2} \{ A'(0) \exp [-y_1^{1/2}(0)x] \\ + B'(0) \exp [-y_2^{1/2}(0)\bar{x}] \} \end{aligned} \quad (4.4.12)$$

$$\begin{aligned} \lim_{t \rightarrow \infty} v(x,t) = \frac{1}{D_1 D_2} \{ C'(0) \exp [-y_1^{1/2}(0) \bar{x}] \\ + E'(0) \exp [-y_2^{1/2}(0) \bar{x}] \} \end{aligned} \quad (4.4.13)$$

where  $A'(0)$ ,  $B'(0)$ ,  $C'(0)$ ,  $E'(0)$  are obtained by putting  $p=0$  in the corresponding expressions (4.4.11).

It is seen that the expressions given by (4.4.12) and (4.4.13) satisfy the steady state form of (4.2.7) with boundary conditions (4.2.10) showing the asymptotic stability of the equilibrium state in this case also.

#### 4.5 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL IN A FINITE HABITAT UNDER RESERVOIR CONDITIONS

To see the effect of convection on the stability of the equilibrium state of the system (4.2.7) under conditions (4.2.10), we consider the case for which

$$\frac{u_1}{D_1} = \frac{u_2}{D_2} \quad (4.5.1)$$

i.e. the ratio of convective velocity to dispersal co-efficient is same for both the species. This problem is biologically reasonable because the species possessing more dispersal ability are likely to have faster convective migration velocity.



Using the following transformations

$$u(x,t) = \exp(\mu_1 x / 2D_1) u_1(x,t) \quad (4.5.2)$$

$$v(x,t) = \exp(\mu_2 x / 2D_2) v_1(x,t)$$

the system (4.2.7) can be written as follows

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= -e_1 u_1 + f v_1 + D_1 \frac{\partial^2 u_1}{\partial x^2} \\ \frac{\partial v_1}{\partial t} &= g u_1 - h_1 v_1 + D_2 \frac{\partial^2 v_1}{\partial x^2} \end{aligned} \quad (4.5.3)$$

where

$$e_1 = e + \mu_1^2 / 4D_1 ; \quad h_1 = h + \mu_2^2 / 4D_2 . \quad (4.5.4)$$

The initial and boundary conditions (4.2.10) reduce to the following form

$$\begin{aligned} u_1(x,0) &= r_1(x), \quad v_1(x,0) = s_1(x) \quad x > 0 \\ u_1(0,t) &= U_1, \quad v_1(0,t) = V_1 \quad t \geq 0 \\ u_1(x,t) &\rightarrow 0, \quad v_1(x,t) \rightarrow 0 \end{aligned} \quad (4.5.5)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat. The functions  $r_1(x)$  and  $s_1(x)$  are defined by

$$\begin{aligned} r_1(x) &= r(x) \exp(-\mu_1 x / 2D_1) \\ s_1(x) &= s(x) \exp(-\mu_2 x / 2D_2) . \end{aligned} \quad (4.5.6)$$

It is noted that the system (4.5.3) with conditions (4.5.5) is of the same form as of the system (4.2.7) for  $u_1 = u_2 = 0$  with conditions (4.2.10) where  $e_1, h_1, r_1(x), s_1(x)$  have been modified according to (4.5.4) and (4.5.6). Thus the solutions of the system (4.2.7) with (4.5.1) can be obtained from case (ii) of Sections 4.3 and 4.4 by making use of (4.5.2), (4.5.4) and (4.5.5) appropriately.

For example, in the case of finite habitat, the solutions of the system (4.2.7) with reservoir conditions (4.2.10) for the case of (4.5.1) can be obtained from (4.3.8) and (4.3.9) by multiplying these equations with  $\exp\left(\frac{u_1 x}{2D_1}\right)$  and  $\exp\left(\frac{u_2 x}{2D_2}\right)$  respectively and replacing  $e$  by  $e_1$ ,  $h$  by  $h_1$ ,  $r(x)$  by  $r_1(x)$ ,  $s(x)$  by  $s_1(x)$ . Thus the corresponding eigen values  $[p'_{1n}, p'_{2n} (n=1,2,3,\dots)]$  for the system (4.5.3) with (4.5.2) would be given by the expressions (4.3.5) by replacing  $e$  by  $e_1$  and  $h$  by  $h_1$  (see appendix). As shown in the appendix, it may be noted that  $p'_{1n}, p'_{2n} (n=1,2,3,\dots)$  are positive and increase with  $u_1$  and  $u_2$ . Hence, in the case of finite habitat, it can be argued that the equilibrium state is stabilized further due to convective migration also and the degree of stability increases with convective velocities.

#### 4.6 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL IN A TWO DIMENSIONAL FINITE HABITAT UNDER RESERVOIR CONDITIONS

Eventhough migration of the species is considered only along a particular direction in the earlier sections, in real situations, the species migrate in all possible directions. In such circumstances, the evolution of the species in a rectangular finite habitat [ $L, M$  being the length of the habitat along  $x, y$ -directions respectively] is governed by the following dynamical equations

$$\begin{aligned} \frac{\partial N_1}{\partial t} + \mu_1 \frac{\partial N_1}{\partial x} + \mu_3 \frac{\partial N_1}{\partial y} = N_1(a_1 - a_{11}N_1 + \frac{a_{12}N_2}{1 + \alpha N_1}) \\ + D_1 \frac{\partial^2 N_1}{\partial x^2} + D_3 \frac{\partial^2 N_1}{\partial y^2} \end{aligned} \quad (4.6.1)$$

$$\begin{aligned} \frac{\partial N_2}{\partial t} + \mu_2 \frac{\partial N_2}{\partial x} + \mu_4 \frac{\partial N_2}{\partial y} = N_2(a_2 - a_{22}N_2 + \frac{a_{21}N_1}{1 + \alpha N_1}) \\ + D_2 \frac{\partial^2 N_2}{\partial x^2} + D_4 \frac{\partial^2 N_2}{\partial y^2} \end{aligned}$$

where  $D_1, D_2, D_3, D_4$  are co-efficients of dispersal of the species and  $\mu_1, \mu_2, \mu_3, \mu_4$  their convective velocities.

As in Section 4.5, consider the case

$$\frac{\mu_1}{D_1} = \frac{\mu_2}{D_2} ; \quad \frac{\mu_3}{D_3} = \frac{\mu_4}{D_4} \quad (4.6.2)$$

i.e. the ratio of convective velocity to dispersal co-efficient

is same for both the species along the particular direction. Similar analysis, as in the previous articles, establishes that the equilibrium state is asymptotically stable in a two dimensional finite habitat under reservoir conditions.

#### 4.7 CONCLUSION

Effects of dispersive and convective migration of the species, which arise due to environmental and ecological gradients, on the linear stability of the equilibrium state for two species system with mutualistic interactions have been investigated by taking into account the functional response in finite and semi-infinite habitats. In both these cases, it has been shown that the equilibrium state which is always stable without migration remains so with dispersal under flux and reservoir boundary conditions.

In the case of a finite habitat, it has also been pointed out that the degree of stability increases with dispersal co-efficients of the species in absence of convective migration. It has been further shown that the effect of convective migration of the species is to stabilize the equilibrium state and the degree of stability increases as convective velocities increase in this case also. It has also been pointed out that the effects of convective and dispersive migration are to stabilize the equilibrium state further in two dimensional finite habitats under reservoir conditions.

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## APPENDIX

From (4.3.5),  $p_{1n}$  and  $p_{2n}$  can be rewritten as

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} (\bar{D}_1 + \bar{D}_2 + e + h) \pm \frac{1}{2} [(\bar{D}_1 - \bar{D}_2 + e - h)^2 + 4fg]^{1/2} \quad (i)$$

where

$$\bar{D}_1 = \frac{n^2 \pi^2}{L^2} D_1, \quad \bar{D}_2 = \frac{n^2 \pi^2}{L^2} D_2 \quad (ii)$$

Since  $eh > fg$ , it is noted from (i) that  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive. To see the behavior of  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) w.r.t.  $D_1, D_2$  and  $L$ , we find

$$\frac{dp_{1n}}{d\bar{D}_1} = \frac{1}{2} \frac{(\bar{D}_1 - \bar{D}_2 + e - h)}{[(\bar{D}_1 - \bar{D}_2 + e - h)^2 + 4fg]^{1/2}} + \frac{1}{2}$$

$$\frac{dp_{1n}}{d\bar{D}_2} = \frac{1}{2} - \frac{1}{2} \frac{(\bar{D}_1 - \bar{D}_2 + e - h)}{[(\bar{D}_1 - \bar{D}_2 + e - h)^2 + 4fg]^{1/2}}.$$

Since  $p_{1n}, \frac{dp_{1n}}{d\bar{D}_1}$  and  $\frac{dp_{1n}}{d\bar{D}_2}$  are positive for  $\bar{D}_1 \geq 0, \bar{D}_2 \geq 0$ ,

it is concluded that  $p_{1n}$  increases with  $\bar{D}_1$  and  $\bar{D}_2$ . Since  $\bar{D}_1, \bar{D}_2$  are proportional to  $D_1, D_2$  and inversely proportional

to  $L$ , it may be noted that  $p_{1n}$  increases with  $D_1$  and  $D_2$  and decreases as  $L$  increases.

Similarly it can also be seen that  $p_{2n}$  increases as  $D_1, D_2$  increase or as  $L$  decreases.

As pointed out earlier, the eigen values  $p'_{1n}, p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) for the system (4.5.3) with (4.5.2) are defined by

$$\begin{pmatrix} p'_{1n} \\ p'_{2n} \end{pmatrix} = \frac{1}{2} (\bar{D}_1 + \bar{D}_2 + e + h + \frac{\bar{\mu}_1}{\bar{D}_1} + \frac{\bar{\mu}_2}{\bar{D}_2}) \pm \frac{1}{2} \left[ (\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})^2 + 4fg \right]^{1/2} \quad (iii)$$

where

$$\bar{\mu}_1 = \frac{n^2 \pi^2}{4L^2} \mu_1^2, \quad \bar{\mu}_2 = \frac{n^2 \pi^2}{4L^2} \mu_2^2. \quad (iv)$$

Since  $eh > fg$ , it is noted from (iii) that  $p'_{1n}, p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive. To see the behavior of  $p'_{1n}, p'_{2n}$  w.r.t.  $\mu_1$  and  $\mu_2$ , we find

$$\begin{aligned} \frac{dp'_{1n}}{d\bar{\mu}_1} &= \frac{1}{2\bar{D}_1} \frac{(\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})}{\left[ (\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})^2 + 4fg \right]^{1/2}} \\ &+ \frac{1}{2\bar{D}_1} \frac{1}{\left[ (\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})^2 + 4fg \right]^{1/2}} \end{aligned}$$



$$\frac{dp'_{1n}}{d\bar{\mu}_2} = \frac{1}{2\bar{D}_2} - \frac{1}{2\bar{D}_2} \frac{(\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})}{[(\bar{D}_1 - \bar{D}_2 + e - h + \frac{\bar{\mu}_1}{\bar{D}_1} - \frac{\bar{\mu}_2}{\bar{D}_2})^2 + 4fg]^{1/2}}.$$

Since  $p'_{1n}$ ,  $\frac{dp'_{1n}}{d\bar{\mu}_1}$  and  $\frac{dp'_{1n}}{d\bar{\mu}_2}$  are positive for  $\bar{D}_1 > 0$  and  $\bar{D}_2 > 0$ , it is concluded that  $p'_{1n}$  increases with  $\bar{\mu}_1$  and  $\bar{\mu}_2$ . Since  $\bar{\mu}_1$ ,  $\bar{\mu}_2$  are proportional to  $\mu_1$ ,  $\mu_2$  respectively, it may be noted that  $p'_{1n}$  increases with  $\mu_1$  and  $\mu_2$ .

Similarly it can also be shown that  $p'_{2n}$  increases with  $\mu_1$  and  $\mu_2$ .

## CHAPTER V

### EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION ON THE LINEAR STABILITY OF PREY-PREDATOR SYSTEM WITH FUNCTIONAL RESPONSE

#### 5.1 INTRODUCTION

In Chapter IV, effects of convective and dispersive migration on the linear stability of the equilibrium state for two species system with mutualistic interactions and functional response have been investigated. Similar effects on prey-predator system are studied in this chapter.

Though the study related to the evolution of interacting species has been quite extensive (May [11], Rapport and Turner [13], Rescigno and Richardson [14], Rosen [15], Scudo and Ziegler [16], Smith [20]), the investigations related to the effects of environment on their co-existence are of recent origin, Chewing [1], Comins and Blatt [2], Gopalsamy [3], Haderler et al. [4], Leung [8], Levin [9], Murtrie [12], Segel and Jackson [17], Segel and Levin [18], Skellam [19], Vandermeer [21]. The effects of environmental and ecological gradients on the evolution of the species can be studied by taking into account their dispersive and convective migration in the habitat, Chewing [1], Comins and Blatt [2],

Gopalsamy [3], Haderler et al. [4], Murtrie [12].

It has been noted that migration in the habitat can lead to stability and coexistence of the species. Levin [9] has presented models of systems showing that stable co-existence is more probable in a heterogeneous environment than in a homogeneous environment. However, dispersal can give rise to instability when an Allee effect is present in the prey dynamics and the predators are highly mobile while the preys are relatively sluggish (Levin [9], Segel and Jackson [17], Segel and Levin [18]). It has also been noted that if the size of an isolated terrestrial habitat is less than a certain critical value, the dispersing populations are open to extinctions which would not occur in the absence of dispersal (Skellam [19]).

It may be noted here that the effects of intra-specific interactions with functional response in prey-predator dynamics have also been investigated (Kazarinoff and Driessche [6], Holling [5], Lin and Kahn [10]), but the effects of convective and dispersive migration on the stability of such systems have not been studied.

Keeping this in view, in the following, effects of dispersive and convective migration of the species on prey-predator interactions in finite and semi-infinite habitats have been investigated by considering the functional response.

## 5.2 BASIC EQUATIONS

Consider the interactions of prey and predator species in a finite or semi-infinite ( $0 \leq x \leq L$  or  $0 \leq x < \infty$ ) habitat with functional response. By taking into account the convective and dispersive migration of the species, the dynamical system describing the interactions (Segel and Levin [18]) can be written as

$$\begin{aligned} \frac{\partial N_1}{\partial t} + u_1 \frac{\partial N_1}{\partial x} &= N_1 \left( a_1 - a_{11} N_1 - a_{12} \frac{N_2}{1 + \alpha N_1} \right) + D_1 \frac{\partial^2 N_1}{\partial x^2} \\ \frac{\partial N_2}{\partial t} + u_2 \frac{\partial N_2}{\partial x} &= N_2 \left( -a_2 + a_{21} \frac{N_1}{1 + \alpha N_1} \right) + D_2 \frac{\partial^2 N_2}{\partial x^2} \end{aligned} \quad (5.2.1)$$

where  $N_1(x, t)$ ,  $N_2(x, t)$  represent the spatial distributions of prey and predator populations at time  $t$  respectively;  $D_1$ ,  $D_2$  are dispersal coefficients;  $u_1$ ,  $u_2$  are migration velocities. The interaction coefficients  $a_1$ ,  $a_2$ ,  $a_{11}$ ,  $a_{12}$ ,  $a_{21}$ ,  $\alpha$  are positive constants. Here the predator's functional response to prey as suggested by Holling [5] is characterised by the term  $(1 + \alpha N_1)^{-1}$  and  $\alpha$  determines the strength of this response.

The nontrivial equilibrium state  $(N_1^*, N_2^*)$  of the system (5.2.1) can be found as

$$N_1^* = \frac{a_2}{a_{21} - a_2 \alpha} ; N_2^* = \frac{a_{21}}{a_{12}(a_{21} - a_2 \alpha)} \left[ a_1 - \frac{a_2 a_{11}}{(a_{21} - a_2 \alpha)} \right]. \quad (5.2.2)$$

It may be noted from (5.2.2) that both  $N_1^*$  and  $N_2^*$  are positive provided  $(a_{21}-a_2\alpha) a_1 > a_2 a_{11} > 0$ .

To investigate the local stability of the equilibrium state  $(N_1^*, N_2^*)$ , we linearise the system (5.2.1) by writing

$$N_1(x,t) = N_1^* + u(x,t) \quad (5.2.3)$$

$$N_2(x,t) = N_2^* + v(x,t)$$

which on substituting in the system (5.2.1) and using (5.2.2) gives

$$\begin{aligned} \frac{\partial u}{\partial t} + \mu_1 \frac{\partial u}{\partial x} &= -eu - fv + D_1 \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} + \mu_2 \frac{\partial v}{\partial x} &= gu + D_2 \frac{\partial^2 v}{\partial x^2} \end{aligned} \quad (5.2.4)$$

where

$$e = \frac{N_1^* [a_{11}(a_{21}+a_2\alpha) - a_1\alpha(a_{21}-a_2\alpha)]}{(1+\alpha N_1^*) (a_{21}-a_2\alpha)}$$

$$f = \frac{a_{12}N_1^*}{(1+\alpha N_1^*)} ; \quad g = \frac{a_{21}N_2^*}{(1+\alpha N_1^*)^2}$$

and  $u(x,t)$ ,  $v(x,t)$  are perturbed population sizes.

From (5.2.5), it may be noted that  $f$  and  $g$  are positive, but  $e$  is positive if  $a_{11} > a_0 \geq 0$  and negative if  $0 < a_{11} < a_0$ , where

$$a_0 = a_1\alpha \frac{(a_{21}-a_2\alpha)}{(a_{21}+a_2\alpha)} \geq 0 \quad \text{for } \alpha \geq 0. \quad (5.2.6)$$

The linearised system (5.2.4) may be associated with the following initial and boundary conditions:

(i) Flux conditions

$$\begin{aligned} u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\ -D_1 \frac{\partial u(0,t)}{\partial x} &= U, \quad -D_2 \frac{\partial v(0,t)}{\partial x} = V & t \geq 0 \\ \frac{\partial u(x,t)}{\partial x} &\rightarrow 0, \quad \frac{\partial v(x,t)}{\partial x} \rightarrow 0 \end{aligned} \quad (5.2.7)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

(ii) Reservoir conditions

$$\begin{aligned} u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\ u(0,t) &= U_1, \quad v(0,t) = V_1 & t \geq 0 \\ u(x,t) &\rightarrow 0, \quad v(x,t) \rightarrow 0 \end{aligned} \quad (5.2.8)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

### 5.3 STABILITY ANALYSIS WITHOUT MIGRATION

If the species are nonmigrative, the system (5.2.4) reduces to

$$\begin{aligned} \frac{du}{dt} &= -eu - fv \\ \frac{dv}{dt} &= gu \end{aligned} \quad (5.3.1)$$

Considering the solutions of (5.3.1) are of the form  $\exp(-\lambda t)$ , the eigen values  $\lambda$  satisfy the following equation

$$\lambda^2 - e\lambda + fg = 0 \quad (5.3.2)$$

which gives

$$\begin{pmatrix} \lambda_1 \\ \lambda_2 \end{pmatrix} = \frac{1}{2} e \pm \frac{1}{2} [e^2 - 4fg]^{1/2}. \quad (5.3.3)$$

It may be noted from (5.3.3) that both  $\lambda_1, \lambda_2$  or their real parts are positive for  $e > 0$  i.e.  $a_{11} > a_0$ , but  $\lambda_1, \lambda_2$  or their real parts are negative for  $e < 0$  i.e.  $a_{11} < a_0$ . Thus the following conclusions may be summarized:

(i) For  $e = 0$  i.e.  $a_{11} = a_0$ , both  $\lambda_1$  and  $\lambda_2$  are purely imaginary and the equilibrium state is neutrally stable.

This is possible even when  $\alpha = 0$  and  $a_{11} = 0$ .

(ii) For  $e > 0$  i.e.  $a_{11} > a_0$ , the equilibrium state is asymptotically stable. This condition is satisfied even for  $\alpha = 0$  because from (5.2.6),  $a_0 = 0$ , giving  $a_{11} > 0$ .

(iii) For  $e < 0$  i.e.  $a_{11} < a_0$ , the equilibrium state is unstable. This can happen even when  $a_{11} = 0$ , but  $\alpha > 0$  [see (5.2.5)].

Results (ii) and (iii) are identical to those obtained by Kazarinoff and Driessche [6].

#### 5.4 STABILITY ANALYSIS WITH DISPERSAL IN A FINITE HABITAT

In the following, we study the stability of the equilibrium state of the system (5.2.4) with dispersal in a finite habitat when flux or reservoir boundary conditions are prescribed ( $u_1 = u_2 = 0$ ).

## Case (i) Flux Conditions

In this case, on solving the system (5.2.4) for  $u_1 = u_2 = 0$  with flux conditions (5.2.7) by using Laplace and finite Fourier cosine transforms, we obtain  $u(x, t)$  and  $v(x, t)$  as

$$\begin{aligned}
 u(x, t) = & \frac{1}{L} \int_0^t \left[ A_0 \exp(-p_{10}T) + B_0 \exp(-p_{20}T) \right] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t \left[ A_n \exp(-p_{1n}T) \right. \right. \\
 & \left. \left. + B_n \exp(-p_{2n}T) \right] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} \left[ F_{10} \exp(-p_{10}t) + F_{20} \exp(-p_{20}t) \right] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ F_{1n} \exp(-p_{1n}t) + F_{2n} \exp(-p_{2n}t) \right] \\
 & \cos \frac{n\pi x}{L} \quad (5.4.1)
 \end{aligned}$$

$$\begin{aligned}
 v(x, t) = & \frac{1}{L} \int_0^t \left[ C_0 \exp(-p_{10}T) + E_0 \exp(-p_{20}T) \right] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t \left[ C_n \exp(-p_{1n}T) \right. \right. \\
 & \left. \left. + E_n \exp(-p_{2n}T) \right] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} \left[ G_{10} \exp(-p_{10}t) + G_{20} \exp(-p_{20}t) \right] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ G_{1n} \exp(-p_{1n}t) + G_{2n} \exp(-p_{2n}t) \right] \\
 & \cos \frac{n\pi x}{L} \quad (5.4.2)
 \end{aligned}$$



where

$$\begin{aligned}
 A_n &= \frac{(p_{1n} - D_2 \sigma_n^2) U + fV}{p_{1n} - p_{2n}} \\
 B_n &= \frac{(D_2 \sigma_n^2 - p_{2n}) U - fV}{p_{1n} - p_{2n}} \\
 C_n &= \frac{(p_{1n} - e - D_1 \sigma_n^2) V - g U}{p_{1n} - p_{2n}} \\
 E_n &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) V + g U}{p_{1n} - p_{2n}} \quad (5.4.3)
 \end{aligned}$$

$$\begin{aligned}
 F_{1n} &= \frac{(p_{1n} - D_2 \sigma_n^2) R_n + f S_n}{p_{1n} - p_{2n}} \\
 F_{2n} &= \frac{(D_2 \sigma_n^2 - p_{2n}) R_n - f S_n}{p_{1n} - p_{2n}} \\
 G_{1n} &= \frac{(p_{1n} - e - D_1 \sigma_n^2) S_n - g R_n}{p_{1n} - p_{2n}} \\
 G_{2n} &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) S_n + g R_n}{p_{1n} - p_{2n}} \quad (5.4.4)
 \end{aligned}$$

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} (D_1 \sigma_n^2 + D_2 \sigma_n^2 + e) \pm \left[ (D_1 \sigma_n^2 - D_2 \sigma_n^2 + e)^2 - 4fg \right]^{1/2} \quad (5.4.5)$$

$\sigma_n = n\pi/L$  and  $(\quad)_0, (\quad)_{10}, (\quad)_{20}$  can be obtained from the corresponding expressions of  $(\quad)_n, (\quad)_{1n}, (\quad)_{2n}$  by putting  $n = 0$ . The constants  $R_n, S_n$  are given by

$$R_n = \int_0^L r(x) \cos \frac{n\pi x}{L} dx$$

$$S_n = \int_0^L s(x) \cos \frac{n\pi x}{L} dx .$$

From (5.3.3), (5.4.5) it may be seen that  $p_{10} = \lambda_1$ ,  $p_{20} = \lambda_2$  and hence  $p_{10}, p_{20}$  or their real parts are positive or negative depending upon whether  $e > 0$  or  $e < 0$ . It may also be seen from (5.4.5) that when  $e = 0$ ,  $p_{10}, p_{20}$  are purely imaginary numbers, but  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) or their real parts are positive. For  $e > 0$ ,  $p_{1n}, p_{2n}$  ( $n = 0, 1, 2, 3, \dots$ ) or their real parts are always positive. However, when  $e < 0$ ,  $p_{10}, p_{20}$  or their real parts are negative, but  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) or their real parts are positive whenever  $(\frac{\pi^2}{L^2} D_1 + e) \geq 0$ . In this case, if  $(\frac{\pi^2}{L^2} D_1 + e) < 0$ , then there may exist a value of  $n$ , say  $n = n_0$ , for which  $p_{2n}$  is negative.

It may also be noted from (5.4.5) that  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) always increase with dispersal coefficients provided  $(D_1 - D_2)$  is fixed.

For  $e > 0$ , as  $p_{1n}, p_{2n}$  ( $n = 0, 1, 2, \dots$ ) or their real parts are positive, the terms in (5.4.1) and (5.4.2) which arise due to initial conditions of (5.2.7) tend to zero as  $t \rightarrow \infty$ . Hence (5.4.1) and (5.4.2) take the following forms as  $t \rightarrow \infty$  provided  $e > 0$ ,

$$\lim_{t \rightarrow \infty} u(x, t) = \frac{1}{L} \left[ \frac{A_0}{p_{10}} + \frac{B_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{A_n}{p_{1n}} + \frac{B_n}{p_{2n}} \right] \cos \frac{n\pi x}{L} \quad (5.4.6)$$

$$\lim_{t \rightarrow \infty} v(x, t) = \frac{1}{L} \left[ \frac{C_0}{p_{10}} + \frac{E_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{C_n}{p_{1n}} + \frac{E_n}{p_{2n}} \right] \cos \frac{n\pi x}{L} . \quad (5.4.7)$$

It may be verified that (5.4.6) and (5.4.7) also satisfy the steady state form of the system (5.2.4) with boundary conditions (5.2.7). Thus it is seen that for  $e > 0$ , the nonstationary solutions (5.4.1) and (5.4.2) tend to the stationary solutions (5.4.6) and (5.4.7) respectively as  $t \rightarrow \infty$  showing that the equilibrium state of the system is asymptotically stable. Further, as  $p_{1n}, p_{2n} (n=1, 2, 3, \dots)$  increase with dispersal coefficients for fixed  $(D_1 - D_2)$  including the case  $D_1 = D_2$ , the degree of stability of the equilibrium state increases with dispersal [see (5.4.1), (5.4.2)] co-efficients. It is also noted from (5.4.6) and (5.4.7) that the steady state solutions form spatial pattern which arise due to nonhomogeneous boundary conditions.

The following conclusions may also be drawn from (5.4.1) and (5.4.2):

- (i) For  $e = 0$ , the equilibrium state is neutrally stable, since  $p_{10}, p_{20}$  are purely imaginary and  $p_{1n}, p_{2n} (n=1, 2, 3, \dots)$  or their real parts are positive.
- (ii) For  $e < 0$ ,  $p_{10}, p_{20}$  or their real parts are negative irrespective of whether  $p_{1n}, p_{2n} (n=1, 2, \dots)$  or their real

parts are positive or negative and hence the equilibrium state is unstable.

Case (ii) Reservoir conditions

On solving the system (5.2.4) for  $u_1 = u_2 = 0$  with conditions (5.2.8), we obtain  $u(x,t)$  and  $v(x,t)$  as

$$\begin{aligned}
 u(x,t) = & \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left\{ \int_0^t \left[ A'_n \exp(-p_{1n}T) \right. \right. \\
 & \left. \left. + B'_n \exp(-p_{2n}T) \right] dT \right\} \sin \frac{n\pi x}{L} \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ F'_{1n} \exp(-p_{1n}t) + F'_{2n} \exp(-p_{2n}t) \right] \sin \frac{n\pi x}{L}
 \end{aligned} \tag{5.4.8}$$

$$\begin{aligned}
 v(x,t) = & \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left\{ \int_0^t \left[ C'_n \exp(-p_{1n}T) + E'_n \exp(-p_{2n}T) \right] dT \right\} \\
 & \sin \frac{n\pi x}{L} \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left[ G'_{1n} \exp(-p_{1n}t) + G'_{2n} \exp(-p_{2n}t) \right] \sin \frac{n\pi x}{L}
 \end{aligned} \tag{5.4.9}$$

where

$$\begin{aligned}
 A'_n &= \frac{(p_{1n} - D_2 \sigma_n^2) D_1 U_1 + f D_2 V_1}{p_{1n} - p_{2n}} \\
 B'_n &= \frac{(D_2 \sigma_n^2 - p_{2n}) D_1 U_1 - f D_2 V_1}{p_{1n} - p_{2n}} \\
 C'_n &= \frac{(p_{1n} - e - D_1 \sigma_n^2) D_2 V_1 - g D_1 U_1}{p_{1n} - p_{2n}} \\
 E'_n &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) D_2 V_1 + g D_1 U_1}{p_{1n} - p_{2n}}
 \end{aligned} \tag{5.4.10}$$

$$\begin{aligned}
F'_{1n} &= \frac{(p_{1n} - D_2 \sigma_n^2) R'_n + f S'_n}{p_{1n} - p_{2n}} \\
F'_{2n} &= \frac{(D_2 \sigma_n^2 - p_{2n}) R'_n - f S'_n}{p_{1n} - p_{2n}} \\
G'_{1n} &= \frac{(p_{1n} - e - D_1 \sigma_n^2) S'_n - g R'_n}{p_{1n} - p_{2n}} \\
G'_{2n} &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) S'_n + g R'_n}{p_{1n} - p_{2n}} \quad (5.4.11)
\end{aligned}$$

$\sigma_n = \frac{n\pi}{L}$  and  $p_{1n}, p_{2n}$  are defined in (5.4.5). The constants  $R'_n$  and  $S'_n$  are given by

$$\begin{aligned}
R'_n &= \int_0^L r(x) \sin \frac{n\pi x}{L} dx \\
S'_n &= \int_0^L s(x) \sin \frac{n\pi x}{L} dx.
\end{aligned}$$

Since  $p_{1n}, p_{2n}$  ( $n=1,2,3,\dots$ ) or their real parts are positive for  $(\frac{\pi^2}{L^2} D_1 + e) \geq 0$ , the terms arising due to initial conditions in each of the expressions (5.4.8) and (5.4.9) tend to zero as  $t \rightarrow \infty$ . Hence (5.4.8) and (5.4.9) take the following forms as  $t \rightarrow \infty$  provided  $(\frac{\pi^2}{L^2} D_1 + e) \geq 0$ ,

$$\lim_{t \rightarrow \infty} u(x, t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{A'_n}{p_{1n}} + \frac{B'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L} \quad (5.4.12)$$

$$\lim_{t \rightarrow \infty} v(x, t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{C'_n}{p_{1n}} + \frac{E'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L}. \quad (5.4.13)$$

It is noted that (5.4.12) and (5.4.13) satisfy the steady state form of (5.2.4) with boundary conditions (5.2.8) showing again the asymptotic stability of the equilibrium state for  $\alpha \geq 0$ , provided  $(\frac{\pi^2}{L^2} D_1 + e) \geq 0$ , under reservoir boundary conditions also and the degree of stability increases as dispersal coefficients increase for fixed  $(D_1 - D_2)$  including the case  $D_1 = D_2$ . In this case also, spatial pattern is formed by steady state solutions due to nonhomogeneous boundary conditions.

The following conclusions may also be drawn from (5.4.8) and (5.4.9):

- (i) For  $e = 0$ , the equilibrium state is asymptotically stable as  $p_{1n}, p_{2n}(n=1,2,3,\dots)$  or their real parts are positive. Thus it may be concluded that the dispersal has the effect to stabilize the otherwise neutrally stable equilibrium state.
- (ii) For  $e > 0$ , the equilibrium state is stable.
- (iii) For  $e < 0$ , the equilibrium state is stable provided  $(\frac{\pi^2}{L^2} D_1 + e) \geq 0$ . Thus it is noted that dispersal has the effect to stabilize even an otherwise unstable equilibrium state. However, when  $(\frac{\pi^2}{L^2} D_1 + e) < 0$ , the equilibrium state may be unstable.

It may be pointed out here that in all these cases the degree of stability increases with dispersal co-efficients provided  $(D_1 - D_2)$  is fixed.

Thus it may be remarked that the stable equilibrium state without dispersal remains stable with dispersal in the case of finite habitat both under flux and reservoir boundary conditions. In the case of flux conditions, the instability of the equilibrium state is not affected by dispersal, while under reservoir conditions the dispersal has the effect to stabilize an otherwise unstable equilibrium state provided certain condition holds.

## 5.5 STABILITY ANALYSIS WITH DISPERSAL IN AN INFINITE HABITAT

In the following, the stability of the equilibrium state of the system (5.2.4) without convection ( $\mu_1 = \mu_2 = 0$ ) is discussed in a semi-infinite habitat under flux and reservoir conditions.

### Case (i) Flux conditions

In this case, on solving the system (5.2.4) for  $\mu_1 = \mu_2 = 0$  with conditions (5.2.7), we obtain

$$\begin{aligned} \bar{u}(x, p) = & \frac{1}{D_1 D_2 p} \left[ \frac{A(p)}{(y_1)^{1/2}} \exp(-y_1^{1/2} x) + \frac{B(p)}{y_2^{1/2}} \exp(-y_2^{1/2} x) \right] \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp(-y_1^{1/2} z)}{y_1^{1/2}} \left[ F_1(p, z+x) + F_1(p, |z-x|) \right] \right. \\ & \left. + \frac{\exp(-y_2^{1/2} z)}{y_2^{1/2}} \left[ F_2(p, z+x) + F_2(p, |z-x|) \right] \right\} dz \quad (5.5.1) \end{aligned}$$

$$\begin{aligned}
\bar{v}(x, p) = & \frac{1}{D_1 D_2 p} \left[ \frac{C(p)}{y_1^{1/2}} \exp(-y_1^{1/2} x) + \frac{E(p)}{y_2^{1/2}} \exp(-y_2^{1/2} x) \right] \\
& + \frac{1}{2 D_1 D_2} \int_0^\infty \left\{ \frac{\exp(-y_1^{1/2} z)}{y_1^{1/2}} \left[ G_1(p, z+x) + G_1(p, |z-x|) \right] \right. \\
& \left. + \frac{\exp(-y_2^{1/2} z)}{y_2^{1/2}} \left[ G_2(p, z+x) + G_2(p, |z-x|) \right] \right\} dz \quad (5.5.2)
\end{aligned}$$

where  $\bar{u}(x, p)$ ,  $\bar{v}(x, p)$  are Laplace transforms of  $u(x, t)$ ,  $v(x, t)$  respectively and

$$A(p) = \frac{(D_2 y_1 - p) U + fV}{y_1 - y_2} ; \quad B(p) = \frac{(p - D_2 y_2) U - fV}{y_1 - y_2} \quad (5.5.3)$$

$$C(p) = \frac{(D_1 y_1 - p - e) V - gU}{y_1 - y_2} ; \quad E(p) = \frac{(p + e - D_1 y_2) V + gU}{y_1 - y_2}$$

$$F_1(p, x) = \frac{(D_2 y_1 - p) r(x) + f s(x)}{y_1 - y_2}$$

$$F_2(p, x) = \frac{(p - D_2 y_2) r(x) - f s(x)}{y_1 - y_2}$$

$$G_1(p, x) = \frac{(D_1 y_1 - p - e) s(x) - g r(x)}{y_1 - y_2}$$

$$G_2(p, x) = \frac{(p + e - D_1 y_2) s(x) + g r(x)}{y_1 - y_2} \quad (5.5.4)$$

$$\begin{pmatrix} y_1(p) \\ y_2(p) \end{pmatrix} = \frac{1}{2} \left( \frac{p+e}{D_1} + \frac{p}{D_2} \right) \pm \frac{1}{2} \left[ \left( \frac{p+e}{D_1} - \frac{p}{D_2} \right)^2 - \frac{4fg}{D_1 D_2} \right]^{1/2}. \quad (5.5.5)$$



It may be noted from (5.5.5) that  $y_1$  and  $y_2$  or their real parts are positive for all values of  $p \geq 0$  provided  $e$  is positive and this fact is used in obtaining the solutions (5.5.1) and (5.5.2). If  $e$  is negative, these solutions are not consistent with the boundary conditions (5.2.7).

To investigate the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$ , we use the following property of Laplace transform (see [7], p. 315),

$$\lim_{t \rightarrow \infty} u(x,t) = \lim_{p \rightarrow 0} p \bar{u}(x,p). \quad (5.5.6)$$

Using (5.5.6) in (5.5.1), (5.5.2), we get,

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{A(0)}{y_1^{1/2}(0)} \exp [-y_1^{1/2}(0)] \right. \\ \left. + \frac{B(0)}{y_2^{1/2}(0)} \exp [-y_2^{1/2}(0)] \right\} \end{aligned} \quad (5.5.7)$$

$$\begin{aligned} \lim_{t \rightarrow \infty} v(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{C(0)}{y_1^{1/2}(0)} \exp [-y_1^{1/2}(0)] \right. \\ \left. + \frac{E(0)}{y_2^{1/2}(0)} \exp [-y_2^{1/2}(0)] \right\} \end{aligned} \quad (5.5.8)$$

provided  $e > 0$ , where  $A(0)$ ,  $B(0)$ ,  $C(0)$ ,  $E(0)$  are obtained by putting  $p = 0$  in the corresponding expressions (5.5.3) and  $y_1(0)$ ,  $y_2(0)$  are the values of  $y_1(p)$ ,  $y_2(p)$  for  $p = 0$ .

It can also be verified that the expressions (5.5.7) and (5.5.8) satisfy the steady state form of the system (5.2.4)

with boundary conditions (5.2.7). Thus it may be noted that for  $e > 0$ , the nonstationary solutions tend to the corresponding stationary solutions as  $t \rightarrow \infty$  showing that the equilibrium state remains asymptotically stable with dispersal under flux boundary conditions. It may also be seen from (5.5.7) and (5.5.8) that the steady state solutions form spatial pattern.

#### Case (ii) Reservoir conditions

As before, on solving the system (5.2.4) for  $u_1 = u_2 = 0$  with conditions (5.2.8), we obtain

$$\begin{aligned} \bar{u}(x,p) = & \frac{1}{D_1 D_2 p} \left[ A'(p) \exp(-y_1^{1/2} x) + B'(p) \exp(-y_2^{1/2} x) \right] \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp(-y_1^{1/2} z)}{y_1^{1/2}} \left[ F_1(p, z+x) - F_1(p, z-x) \right] \right. \\ & \left. + \frac{\exp(-y_2^{1/2} z)}{y_2^{1/2}} \left[ F_2(p, z+x) - F_2(p, z-x) \right] \right\} dz \end{aligned} \quad (5.5.9)$$

$$\begin{aligned} \bar{v}(x,p) = & \frac{1}{D_1 D_2 p} \left[ C'(p) \exp(-y_1^{1/2} x) + E'(p) \exp(-y_2^{1/2} x) \right] \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp(-y_1^{1/2} z)}{y_1^{1/2}} \left[ G_1(p, z+x) - G_1(p, z-x) \right] \right. \\ & \left. + \frac{\exp(-y_2^{1/2} z)}{y_2^{1/2}} \left[ G_2(p, z+x) - G_2(p, z-x) \right] \right\} dz \end{aligned} \quad (5.5.10)$$

where  $\bar{u}(x,p)$ ,  $\bar{v}(x,p)$  are Laplace transforms of  $u(x,t)$ ,  $v(x,t)$  respectively and

$$\begin{aligned}
 A'(p) &= \frac{(D_2 y_1 - p) D_1 U_1 + f D_2 V_1}{y_1 - y_2} \\
 B'(p) &= \frac{(p - D_2 y_2) D_1 U_1 - f D_2 V_1}{y_1 - y_2} \\
 C'(p) &= \frac{(D_1 y_1 - p - e) D_2 V_1 - g D_1 U_1}{y_1 - y_2} \\
 E'(p) &= \frac{(p + e - D_1 y_2) D_2 V_1 + g D_1 U_1}{y_1 - y_2} .
 \end{aligned} \tag{5.5.11}$$

$F_1(p,x)$ ,  $F_2(p,x)$ ,  $G_1(p,x)$ ,  $G_2(p,x)$  are defined in (5.5.4) and  $y_1(p)$ ,  $y_2(p)$  are defined in (5.5.5).

Here it should be noted that the expressions given by (5.5.9) and (5.5.10) are consistent with the boundary conditions provided  $e > 0$ .

To investigate the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$  as  $t \rightarrow \infty$ , we use the property of Laplace transform given by (5.5.6) in (5.5.9) and (5.5.10), for  $e > 0$ , to get

$$\begin{aligned}
 \lim_{t \rightarrow \infty} u(x,t) &= \frac{1}{D_1 D_2} \{ A'(0) \exp [-y_1^{1/2}(0) x] \\
 &\quad + B'(0) \exp [-y_2^{1/2}(0) x] \}
 \end{aligned} \tag{5.5.12}$$

$$\begin{aligned}
 \lim_{t \rightarrow \infty} v(x,t) &= \frac{1}{D_1 D_2} \{ C'(0) \exp [-y_1^{1/2}(0) x] \\
 &\quad + E'(0) \exp [-y_2^{1/2}(0) x] \}
 \end{aligned} \tag{5.5.13}$$

where  $A'(0)$ ,  $B'(0)$ ,  $C'(0)$ ,  $E'(0)$  are obtained by putting  $p = 0$  in the corresponding expressions given by (5.5.11).

It is seen that the expressions (5.5.12) and (5.5.13) satisfy the steady state form of the system (5.2.4) with boundary conditions (5.2.8) showing that the equilibrium state remains stable for  $e > 0$ . In this case also, spatial pattern arises due to nonhomogeneous boundary conditions which may be noticed from (5.5.12) and (5.5.13).

## 5.6 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL IN A FINITE HABITAT UNDER RESERVOIR CONDITIONS

To study the effect of convection on the stability of the equilibrium state of the system (5.2.4) with conditions (5.2.8), we consider the case

$$\frac{u_1}{D_1} = \frac{u_2}{D_2} \quad (5.6.1)$$

which means that the ratio of convective velocity to dispersal co-efficient is same for both the species.

By using the transformations

$$\begin{aligned} u(x,t) &= \exp\left(\frac{u_1 x}{2D_1}\right) u_1(x,t) \\ v(x,t) &= \exp\left(\frac{u_2 x}{2D_2}\right) v_1(x,t) \end{aligned} \quad (5.6.2)$$

the system (5.2.4) can be written as follows

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= -e_1 u_1 - f v_1 + D_1 \frac{\partial^2 u_1}{\partial x^2} \\ \frac{\partial v_1}{\partial t} &= g u_1 - h_1 v_1 + D_2 \frac{\partial^2 v_1}{\partial x^2}\end{aligned}\quad (5.6.3)$$

where

$$e_1 = e + \frac{\mu_1^2}{4D_1}, \quad h_1 = \frac{\mu_2^2}{4D_2}. \quad (5.6.4)$$

The initial and boundary conditions (5.2.8) reduce to the following forms

$$\begin{aligned}u_1(x, 0) &= r_1(x), \quad v_1(x, 0) = s_1(x) \quad x > 0 \\ u_1(0, t) &= U_1, \quad v_1(0, t) = V_1 \quad t \geq 0 \\ u_1(x, t) &\rightarrow 0, \quad v_1(x, t) \rightarrow 0\end{aligned}\quad (5.6.5)$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

The functions  $r_1(x)$  and  $s_1(x)$  are given by

$$\begin{aligned}r_1(x) &= r(x) \exp(-\mu_1 x/2D_1) \\ s_1(x) &= s(x) \exp(-\mu_2 x/2D_2).\end{aligned}\quad (5.6.6)$$

It is noted that the system (5.6.3) with conditions (5.6.5) is almost the same as that of system (5.2.4) for  $\mu_1 = \mu_2 = 0$  with conditions (5.2.8), where  $e_1$ ,  $h_1$ ,  $r_1(x)$ ,  $s_1(x)$  are defined in (5.6.4) and (5.6.6). Hence the solutions of the system (5.2.4) with conditions (5.2.8) are obtained as in case (ii) of Sections 5.4 and 5.5 by making use of (5.6.2),

(5.6.4) and (5.6.5) appropriately and the stability of the equilibrium state is discussed as before.

For example, in the case of finite habitat, the stability of the equilibrium state is determined by the nature of eigen values  $p'_{1n}$ ,  $p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) where

$$\begin{pmatrix} p'_{1n} \\ p'_{2n} \end{pmatrix} = \frac{1}{2} \left( \frac{n^2 \pi^2}{L^2} D_1 + \frac{n^2 \pi^2}{L^2} D_2 + e + \frac{\mu_1^2}{4D_1} + \frac{\mu_2^2}{4D_2} \right) \pm \frac{1}{2} \left[ \left( \frac{n^2 \pi^2}{L^2} D_1 - \frac{n^2 \pi^2}{L^2} D_2 + e + \frac{\mu_1^2}{4D_1} - \frac{\mu_2^2}{4D_2} \right)^2 - 4fg \right]^{1/2}. \quad (5.6.7)$$

It may be noted from (5.6.7) that  $p'_{1n}$ ,  $p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) or their real parts are positive provided

$$\frac{\mu_1^2}{4D_1} + \frac{\pi^2}{L^2} D_1 + e \geq 0 \quad (5.6.8)$$

and hence the equilibrium state is asymptotically stable under the condition (5.6.8).

From (5.6.8), we can draw the following conclusions :

- (i) For  $e \geq 0$ , the equilibrium state is asymptotically stable with dispersal and convection.
- (ii) For  $e < 0$ , the convective migration has the effect to stabilize an otherwise unstable equilibrium state with dispersal because condition (5.6.8) may be satisfied, but  $(\frac{\pi^2}{L^2} D_1 + e) < 0$ .

It may be noted from the above analysis that the convective migration in the direction of some environmental gradient can enhance the stability of the equilibrium state for prey-predator system with functional response.

### 5.7 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL IN A TWO DIMENSIONAL FINITE HABITAT UNDER RESERVOIR CONDITIONS

In the earlier sections, we considered the migration of the species only along x-direction for simplicity. In real situations, the species migrate in all possible directions in the habitat. The dynamical system governing the evolution of the species in a rectangular finite habitat [ $L, M$  being the lengths of the habitat along x,y-directions respectively] can be written as

$$\begin{aligned} \frac{\partial N_1}{\partial t} + \mu_1 \frac{\partial N_1}{\partial x} + \mu_3 \frac{\partial N_1}{\partial y} = N_1 \left( a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1} \right) \\ + D_1 \frac{\partial^2 N_1}{\partial x^2} + D_3 \frac{\partial^2 N_1}{\partial y^2} \quad (5.7.1) \end{aligned}$$

$$\frac{\partial N_2}{\partial t} + \mu_2 \frac{\partial N_2}{\partial x} + \mu_4 \frac{\partial N_2}{\partial y} = N_2 \left( -a_2 + \frac{a_{21}N_1}{1+\alpha N_1} \right) + D_2 \frac{\partial^2 N_2}{\partial x^2} + D_4 \frac{\partial^2 N_2}{\partial y^2}$$

where  $D_1, D_2, D_3, D_4$  denote the dispersal co-efficients of the species;  $\mu_1, \mu_2, \mu_3, \mu_4$  denote their convective velocities.

As in the previous section, consider the case in which

$$\frac{\mu_1}{D_1} = \frac{\mu_2}{D_2} ; \frac{\mu_3}{D_3} = \frac{\mu_4}{D_4} \quad (5.7.2)$$

i.e. the ratio of convective velocity to dispersal co-efficient is same for both the species along a particular direction.

Analysing the stability of the equilibrium state  $(N_1^*, N_2^*)$  as in the earlier sections, it may be seen that the equilibrium state is asymptotically stable provided

$$\left( \frac{\mu_1^2}{4D_1} + \frac{\mu_3^2}{4D_3} + \frac{\pi^2}{L^2} D_1 + \frac{\pi^2}{M^2} D_3 + e \right) \geq 0. \quad (5.7.3)$$

Comparing (5.7.3) with (5.6.8), it is noted that the equilibrium state which is unstable in one dimensional habitat can become stable in two dimensional finite habitat provided the inequality (5.7.3) holds.

## 5.8 CONCLUSION

Effects of dispersive and convective migration of the species on the linear stability of the equilibrium state of prey-predator system have been investigated by taking into account the predator's functional response to prey in finite and semi-infinite habitats. It has been shown that the functional response has destabilizing effect. In the case of a finite habitat, it has been noted that an otherwise stable equilibrium state remains stable with dispersal both under flux and reservoir conditions and the degree of stability increases with dispersal co-efficients when their difference is fixed. In this case, it is also shown that an unstable equilibrium state remains unstable with dispersal under flux



conditions; but dispersal has the effect to stabilize an otherwise unstable equilibrium state under reservoir boundary conditions. Even in the case of semi-infinite habitat, an otherwise stable equilibrium state remains so with dispersal. It has also been seen in the above cases that the steady state population of the species depends only upon nonhomogeneous boundary conditions and form a nonuniform spatial pattern.

It has been shown that the effect of convective migration is not only to stabilize the already stable equilibrium state with dispersal, but also to stabilize even an otherwise unstable equilibrium state with dispersal in the case of finite habitat.

Further, it has been pointed out that the equilibrium state which is unstable in one dimensional habitat may become stable in two dimensional finite habitat under reservoir conditions.

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## CHAPTER VI

### EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION ON THE LINEAR STABILITY OF TWO COMPETING SPECIES SYSTEM WITH FUNCTIONAL RESPONSE

#### 6.1 INTRODUCTION

In Chapters IV and V, effects of convective and dispersive migration on the linear stability of systems of two interacting species with functional response in cases of mutualistic, prey-predator interactions respectively have been discussed. In this chapter, similar investigations are carried out for two competing species model.

The evolution, stability and continued co-existence of population over time of two competing species have been extensively studied, Frauer [1], Gomatham and Mac Donald [2], Leou and Tumpson [8], May [11], Maynard Smith [12], Rescigno and Richardson [13]. By considering a model of two competing preys and one predator having switching property of predation, Teramoto et al. [15] have demonstrated that the predation pressure has a stabilizing effect on the community of competitive species. A model has been presented by Hallam [5] showing that proto co-operative species can drive a stable competitive community to extinction. It may however be noted here that the effect of functional response

on prey-predator system has been studied, but such effects have not been investigated in the case of competition model (Kazarinoff and Driessche [7], Lin and Kahn [10], May [11]).

It is also seen that the effect of dispersal on the dynamics of biological populations has been investigated by several workers, Gopalsamy [3], Haderler et al. [4], Harada and Fukao [6], Levin [9], Segel and Levin [14]. Effect of boundary conditions on the dynamics of dispersive species in a linear habitat has been investigated by Gopalsamy [3] and Haderler et al. [4] in cases of competition and prey-predator models respectively. Harada and Fukao [6] have investigated the co-existence of two competing species in a linear habitat of finite length by considering Volterra-Verhulst model. It should be pointed out here that the effects of convective and dispersive migration on the stability of the equilibrium state for system of two competing species with functional response have not yet been investigated.

Keeping the above in view, in the following, the effects of convective and dispersive migration on the linear stability of the equilibrium state for two competing species system with functional response have been studied in finite and semi-infinite habitats under flux and reservoir conditions.

## 6.2 BASIC EQUATIONS

Consider the evolution of two competing species with intraspecific interactions and functional response in a linear one dimensional finite ( $0 \leq x \leq L$ ) or semi-infinite ( $0 \leq x < \infty$ ) habitat which are capable of migration along  $x$ -direction. By taking into account the effects of convective and dispersive migration of the species, the dynamical system describing their interactions (Kazarinoff and Driessche [7], Segel and Levin [14]) can be written as

$$\begin{aligned} \frac{\partial N_1}{\partial t} + \mu_1 \frac{\partial N_1}{\partial x} &= N_1(a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1}) + D_1 \frac{\partial^2 N_1}{\partial x^2} \\ \frac{\partial N_2}{\partial t} + \mu_2 \frac{\partial N_2}{\partial x} &= N_2(a_2 - a_{22}N_2 - \frac{a_{21}N_1}{1+\alpha N_1}) + D_2 \frac{\partial^2 N_2}{\partial x^2} \end{aligned} \quad (6.2.1)$$

where  $N_1(x,t)$ ,  $N_2(x,t)$  represent the population distributions of two species at time  $t$ ;  $D_1$ ,  $D_2$  their co-efficients of dispersal;  $\mu_1$ ,  $\mu_2$  their convective migration velocities. The interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, a_{22}$  and  $\alpha$  are positive constants. The term  $(1+\alpha N_1)^{-1}$  stands for the functional response in the model (see [7], [11]) and  $\alpha$  determines the strength of this response.

The nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (6.2.1) is given by

$$\begin{aligned}
 a_1 - a_{11}N_1^* - \frac{a_{12}N_2^*}{1 + \alpha N_1^*} &= 0 \\
 a_2 - a_{22}N_2^* - \frac{a_{21}N_1^*}{1 + \alpha N_1^*} &= 0 .
 \end{aligned}
 \tag{6.2.2}$$

Eliminating  $N_2^*$  from (6.2.2), we get the following cubic equation for  $N_1^*$

$$\begin{aligned}
 a_{11}a_{22}\alpha^2 N_1^{*3} - a_{22}\alpha(a_1\alpha - 2a_{11})N_1^{*2} \\
 + [a_{11}a_{22} - 2a_1\alpha - a_{22} - a_{12}(a_{21} - a_2\alpha)]N_1^* \\
 + a_2a_{12} - a_1a_{22} = 0 .
 \end{aligned}
 \tag{6.2.3}$$

It may be noted here that for  $\alpha = 0$ , the nontrivial positive equilibrium state of the system (6.2.1) is stable provided

$$\frac{a_{22}}{a_{12}} > \frac{a_2}{a_1} > \frac{a_{21}}{a_{11}} .
 \tag{6.2.4}$$

In the case  $\alpha > 0$ , for  $N_1^*$  and  $N_2^*$  to be positive, from (6.2.2) and keeping in view (6.2.4), we have

$$\frac{a_2}{a_{21} - a_2\alpha} > \frac{a_1}{a_{11}} > N_1^*
 \tag{6.2.5}$$

giving

$$a_{21} > a_2\alpha .
 \tag{6.2.6}$$

It is also noted from (6.2.3) that there exists only one positive value for  $N_1^*$  and  $N_2^*$  under (6.2.4) and (6.2.6).

To analyse the local stability of the equilibrium state  $(N_1^*, N_2^*)$ , we linearise the system (6.2.1) by writing

$$\begin{aligned} N_1(x, t) &= N_1^* + u(x, t) \\ N_2(x, t) &= N_2^* + v(x, t) \end{aligned} \quad (6.2.7)$$

in the system (6.2.1) and we neglect the higher order terms to get

$$\begin{aligned} \frac{\partial u}{\partial t} + \mu_1 \frac{\partial u}{\partial x} &= -eu - fv + D_1 \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} + \mu_2 \frac{\partial v}{\partial x} &= -gu - hv + D_2 \frac{\partial^2 v}{\partial x^2} \end{aligned} \quad (6.2.8)$$

where  $u, v$  are small perturbed population distributions and

$$\begin{aligned} e &= \frac{N_1^*}{(1 + \alpha N_1^*)} (a_{11} - a_1 \alpha + 2a_{11} \alpha N_1^*) \\ f &= \frac{a_{12} N_1^*}{1 + \alpha N_1^*} \\ g &= \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2} ; \quad h = a_{22} N_2^* \end{aligned} \quad (6.2.9)$$

which are positive in view of (6.2.4) and (6.2.6).

The system (6.2.8) is associated with the following initial and boundary conditions:



(i) Flux conditions

$$\begin{aligned}
 u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\
 -D_1 \frac{\partial u(0,t)}{\partial x} &= U, \quad -D_2 \frac{\partial v(0,t)}{\partial x} = V & t \geq 0 \\
 \frac{\partial u(x,t)}{\partial x} &\rightarrow 0, \quad \frac{\partial v(x,t)}{\partial x} \rightarrow 0
 \end{aligned} \tag{6.2.10}$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

(ii) Reservoir conditions

$$\begin{aligned}
 u(x,0) &= r(x), \quad v(x,0) = s(x) & x > 0 \\
 u(0,t) &= U_1, \quad v(0,t) = V_1 & t \geq 0 \\
 u(x,t) &\rightarrow 0, \quad v(x,t) \rightarrow 0
 \end{aligned} \tag{6.2.11}$$

as  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat.

### 6.3 STABILITY ANALYSIS WITHOUT MIGRATION

If the species are nonmigrative, the system (6.2.8) reduces to

$$\begin{aligned}
 \frac{du}{dt} &= -eu-fv \\
 \frac{dv}{dt} &= -gu-hv
 \end{aligned} \tag{6.3.1}$$

Considering the solutions of (6.3.1) to be of the form  $\exp(-\lambda t)$ , the eigen values  $\lambda_1, \lambda_2$  satisfying the equation

$$\lambda^2 - (e+h)\lambda + eh-fg = 0 \tag{6.3.2}$$

are given by

$$\begin{pmatrix} \lambda_1 \\ \lambda_2 \end{pmatrix} = \frac{1}{2} (e+h) \pm \frac{1}{2} [(e-h)^2 + 4fg]^{1/2}. \quad (6.3.3)$$

Since  $e, f, g$  and  $h$  are positive,  $\lambda_1$  is always positive and  $\lambda_2$  is positive iff

$$eh > fg \quad (6.3.4)$$

which from (6.2.9) gives

$$a_{22} [a_{11} - \alpha(a_1 - a_{11}N_1^*) + a_{11}\alpha N_1^*] (1 + \alpha N_1^*)^2 > a_{12}a_{21}. \quad (6.3.5)$$

Thus it is concluded that the equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable provided (6.3.5) is satisfied.

It may be remarked here that if the set of parametric values consistent with (6.2.4) and (6.2.6) are such that

$$N_1^* \geq \frac{a_1}{2a_{11}} \quad (6.3.6)$$

then (6.3.5) holds automatically.

As  $\frac{a_1}{a_{11}} > N_1^*$  [see (6.2.5)], it is also remarked that the inequality (6.3.5) may not be valid for a particular set of parametric values, though the conditions (6.2.4) and (6.2.6) are satisfied showing that the functional response has destabilizing effect.

#### 6.4 STABILITY ANALYSIS WITH DISPERSAL IN A FINITE HABITAT

In the following, we examine the stability of the equilibrium state with dispersal in a finite habitat under

flux and reservoir boundary conditions ( $u_1=u_2=0$ ).

Case (i) Flux conditions

On solving the system (6.2.8) for  $u_1=u_2=0$  with flux conditions (6.2.10), we obtain  $u(x,t)$  and  $v(x,t)$  as

$$\begin{aligned}
 u(x,t) = & \frac{1}{L} \int_0^t [A_0 \exp(-p_{10}T) + B_0 \exp(-p_{20}T)] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t [A_n \exp(-p_{1n}T) + B_n \exp(-p_{2n}T)] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} [F_{10} \exp(-p_{10}t) + F_{20} \exp(-p_{20}t)] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} [F_{1n} \exp(-p_{1n}t) + F_{2n} \exp(-p_{2n}t)] \cos \frac{n\pi x}{L} \quad (6.4.1)
 \end{aligned}$$

$$\begin{aligned}
 v(x,t) = & \frac{1}{L} \int_0^t [C_0 \exp(-p_{10}T) + E_0 \exp(-p_{20}T)] dT \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} \left\{ \int_0^t [C_n \exp(-p_{1n}T) + E_n \exp(-p_{2n}T)] dT \right\} \cos \frac{n\pi x}{L} \\
 & + \frac{1}{L} [G_{10} \exp(-p_{10}t) + G_{20} \exp(-p_{20}t)] \\
 & + \frac{2}{L} \sum_{n=1}^{\infty} [G_{1n} \exp(-p_{1n}t) + G_{2n} \exp(-p_{2n}t)] \cos \frac{n\pi x}{L} \quad (6.4.2)
 \end{aligned}$$

where

$$\begin{aligned}
A_n &= \frac{(p_{1n} - h - D_2 \sigma_n^2) U + fV}{p_{1n} - p_{2n}} \\
B_n &= \frac{(D_2 \sigma_n^2 + h - p_{2n}) U - fV}{p_{1n} - p_{2n}} \\
C_n &= \frac{(p_{1n} - e - D_1 \sigma_n^2) V + gU}{p_{1n} - p_{2n}} \\
E_n &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) V - gU}{p_{1n} - p_{2n}}
\end{aligned} \tag{6.4.3}$$

$$\begin{aligned}
F_{1n} &= \frac{(p_{1n} - h - D_2 \sigma_n^2) R_n + f S_n}{p_{1n} - p_{2n}} \\
F_{2n} &= \frac{(D_2 \sigma_n^2 + h - p_{2n}) R_n - f S_n}{p_{1n} - p_{2n}} \\
G_{1n} &= \frac{(p_{1n} - e - D_1 \sigma_n^2) S_n + g R_n}{p_{1n} - p_{2n}} \\
G_{2n} &= \frac{(D_1 \sigma_n^2 + e - p_{2n}) S_n - g R_n}{p_{1n} - p_{2n}}
\end{aligned} \tag{6.4.4}$$

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} (D_1 \sigma_n^2 + D_2 \sigma_n^2 + e + h) \pm \frac{1}{2} [(D_1 \sigma_n^2 - D_2 \sigma_n^2 + e - h)^2 + 4fg]^{1/2} \tag{6.4.5}$$

$\sigma_n = \frac{n\pi}{L}$  and  $( )_0, ( )_{10}, ( )_{20}$  are obtained from the corresponding expressions of  $( )_n, ( )_{1n}, ( )_{2n}$  by putting  $n = 0$ . The constants  $R_n, S_n$  are given by

$$R_n = \int_0^L r(x) \cos \frac{n\pi x}{L} dx$$

$$S_n = \int_0^L s(x) \cos \frac{n\pi x}{L} dx.$$

It may be noted from (6.3.3) and (6.4.5) that  $p_{10} = \lambda_1$ ,  $p_{20} = \lambda_2$ . It may also be seen from (6.4.5) that  $p_{1n}(n=1,2,3,\dots)$  are always positive and  $p_{2n}(n=1,2,3,\dots)$  are positive if

$$\left(\frac{D_1\pi^2}{L^2} + e\right) \left(\frac{D_2\pi^2}{L^2} + h\right) > fg. \quad (6.4.6)$$

It has also been shown that  $p_{1n}, p_{2n}(n = 1,2,3,\dots)$  increase with dispersal co-efficients (see appendix, Chapter IV).

If (6.3.4) holds i.e.  $p_{1n}, p_{2n}(n=0,1,2,3,\dots)$  are positive, the nonstationary solutions (6.4.1) and (6.4.2) converge to the following forms as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(x,t) = \frac{1}{L} \left[ \frac{A_0}{p_{10}} + \frac{B_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{A_n}{p_{1n}} + \frac{B_n}{p_{2n}} \right] \cos \frac{n\pi x}{L} \quad (6.4.7)$$

$$\lim_{t \rightarrow \infty} v(x,t) = \frac{1}{L} \left[ \frac{C_0}{p_{10}} + \frac{E_0}{p_{20}} \right] + \frac{2}{L} \sum_{n=1}^{\infty} \left[ \frac{C_n}{p_{1n}} + \frac{E_n}{p_{2n}} \right] \cos \frac{n\pi x}{L}. \quad (6.4.8)$$

Since  $p_{1n}, p_{2n}(n=1,2,3,\dots)$  are positive and increase with dispersal co-efficients, the rate of convergence increases with dispersal co-efficients. Further, as (6.4.7) and (6.4.8) satisfy the steady state form of the system (6.2.8) with boundary conditions (6.2.10), the equilibrium state is asymptotically stable for  $\alpha \geq 0$  and the degree of stability increases with dispersal co-efficients. It can also be seen

from (6.4.7) and (6.4.8) that the steady state solutions form spatial pattern which arise due to nonhomogeneous boundary conditions.

Even if the inequality (6.3.4) does not hold, the equilibrium state can become stable provided  $D_1 = D_2$  and the initial and boundary conditions satisfy the following relations

$$\begin{aligned} (h - \lambda_2) U &= fV \\ \text{or } (e - \lambda_2) V &= gU \end{aligned} \tag{6.4.9}$$

$$\begin{aligned} (h - \lambda_2) r(x) &= f s(x) \\ \text{or } (e - \lambda_2) s(x) &= g r(x) \end{aligned} \tag{6.4.10}$$

which are likely to be satisfied under very special ecological circumstances, where  $\lambda_2$  is defined in (6.3.3). In general, such conditions may not be applicable to realistic habitats.

Case (ii) Reservoir conditions

Again in this case, on solving the system (6.2.8) with conditions (6.2.11), we obtain

$$\begin{aligned} u(x, t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \int_0^t \left[ A'_n \exp(-p_{1n}T) \right. \\ \left. + B'_n \exp(-p_{2n}T) \right] dT \sin \frac{n\pi x}{L} \\ + \frac{2}{L} \sum_{n=1}^{\infty} \left[ F'_{1n} \exp(-p_{1n}t) + F'_{2n} \exp(-p_{2n}t) \right] \sin \frac{n\pi x}{L} \end{aligned} \tag{6.4.11}$$

$$R'_n = \int_0^L r(x) \sin \frac{n\pi x}{L} dx$$

$$S'_n = \int_0^L s(x) \sin \frac{n\pi x}{L} dx.$$

If (6.4.6) is satisfied, as  $p_{1n}, p_{2n} (n=1,2,3,\dots)$  are positive, the nonstationary solutions (6.4.11) and (6.4.12) converge to the following forms as  $t \rightarrow \infty$

$$\lim_{t \rightarrow \infty} u(x,t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{A'_n}{p_{1n}} + \frac{B'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L} \quad (6.4.15)$$

$$\lim_{t \rightarrow \infty} u(x,t) = \frac{2\pi}{L^2} \sum_{n=1}^{\infty} n \left[ \frac{C'_n}{p_{1n}} + \frac{E'_n}{p_{2n}} \right] \sin \frac{n\pi x}{L} \quad (6.4.16)$$

and the rate of convergence increases with dispersal co-efficients. Since (6.4.15) and (6.4.16) are steady state solutions of the system (6.2.8) with boundary conditions (6.2.11), the equilibrium state is asymptotically stable for  $\alpha \geq 0$  and the degree of stability increases with dispersal co-efficients under reservoir conditions also. It is further noted that the steady state solutions give rise to spatial pattern.

Keeping in view the inequalities (6.3.4) and (6.4.6), it is observed that the stable equilibrium state without dispersal remains so with dispersal and the effect of dispersal is also to stabilize even an otherwise unstable equilibrium state without dispersal under (6.4.6).

Even if the inequality (6.4.6) does not hold, the equilibrium state can become stable provided  $D_1 = D_2$ , the initial and boundary conditions satisfy the relations such as (6.4.10) and

$$\begin{aligned} (n-\lambda_2) U_1 &= fV_1 \\ \text{or } (e-\lambda_2) V_1 &= gU_1 \end{aligned} \quad (6.4.17)$$

which are not applicable to realistic situations.

## 6.5 STABILITY ANALYSIS WITH DISPERSAL IN AN INFINITE HABITAT

In the following, the stability of the equilibrium state without convection ( $\mu_1 = \mu_2 = 0$ ) is analysed in a semi-infinite habitat under flux and reservoir conditions.

### Case (i) Flux conditions

On solving the system (6.2.8) for  $\mu_1 = \mu_2 = 0$  with conditions (6.2.10), we obtain

$$\begin{aligned} \bar{u}(x,p) &= \frac{1}{D_1 D_2 p} \left\{ \frac{A(p)}{y_1^{1/2}(p)} \exp[-y_1^{1/2}(p)x] \right. \\ &\quad \left. + \frac{B(p)}{y_2^{1/2}(p)} \exp[-y_2^{1/2}(p)x] \right\} \\ &+ \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp[-y_1^{1/2}(p)z]}{y_1^{1/2}(p)} [F_1(p, z+x) + F_1(p, |z-x|)] \right. \\ &\quad \left. + \frac{\exp[-y_2^{1/2}(p)z]}{y_2^{1/2}(p)} [F_2(p, z+x) + F_2(p, |z-x|)] \right\} dz \end{aligned} \quad (6.5.1)$$



$$\begin{aligned}
\bar{v}(x, p) = & \frac{1}{D_1 D_2 p} \left\{ \frac{C(p)}{y_1^{1/2}(p)} \exp [-y_1^{1/2}(p)x] \right. \\
& + \frac{E(p)}{y_2^{1/2}(p)} \exp [-y_2^{1/2}(p)x] \left. \right\} \\
& + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp [-y_1^{1/2}(p)z]}{y_1^{1/2}(p)} [G_1(p, z+x) + G_1(p, |z-x|)] \right. \\
& + \frac{\exp [-y_2^{1/2}(p)z]}{y_2^{1/2}(p)} [G_2(p, z+x) + G_2(p, |z-x|)] \left. \right\} dz
\end{aligned} \tag{6.5.2}$$

where  $\bar{u}(x, p)$ ,  $\bar{v}(x, p)$  are Laplace transforms of  $u(x, t)$ ,  $v(x, t)$  respectively and

$$\begin{aligned}
A(p) &= \frac{(D_2 y_1 - p - h)U + fV}{y_1 - y_2}; \quad B(p) = \frac{(p + h - D_2 y_2)U - fV}{y_1 - y_2} \\
C(p) &= \frac{(D_1 y_1 - p - e)V + gU}{y_1 - y_2}; \quad E(p) = \frac{(p + e - D_1 y_2)V - gU}{y_1 - y_2}
\end{aligned} \tag{6.5.3}$$

$$\begin{aligned}
F_1(p, x) &= \frac{(D_2 y_1 - p - h) r(x) + f s(x)}{y_1 - y_2} \\
F_2(p, x) &= \frac{(p + h - D_2 y_2) r(x) - f s(x)}{y_1 - y_2} \\
G_1(p, x) &= \frac{(D_1 y_1 - p - e) s(x) + g r(x)}{y_1 - y_2} \\
G_2(p, x) &= \frac{(p + e - D_1 y_2) s(x) - g r(x)}{y_1 - y_2}
\end{aligned} \tag{6.5.4}$$

$$\begin{pmatrix} y_1(p) \\ y_2(p) \end{pmatrix} = \frac{1}{2} \left( \frac{p+e}{D_1} + \frac{p+h}{D_2} \right) \pm \frac{1}{2} \left[ \left( \frac{p+e}{D_1} - \frac{p+h}{D_2} \right)^2 + \frac{4fg}{D_1 D_2} \right]^{1/2}. \quad (6.5.5)$$

It may be noted from (6.5.5) that  $y_1$  and  $y_2$  are positive for all values of  $p \geq 0$  provided  $eh > fg$  and this fact is used in obtaining the solutions (6.5.1) and (6.5.2).

To know the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$  as  $t \rightarrow \infty$ , the following property of Laplace transform

$$\lim_{t \rightarrow \infty} u(x,t) = \lim_{p \rightarrow 0} p \bar{u}(x,p) \quad (6.5.6)$$

is used in (6.5.1) and (6.5.2) to get

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{A(0)}{y_1^{1/2}(0)} \exp \left[ -y_1^{1/2}(0) x \right] \right. \\ \left. + \frac{B(0)}{y_2^{1/2}(0)} \exp \left[ -y_2^{1/2}(0) x \right] \right\} \quad (6.5.7) \end{aligned}$$

$$\begin{aligned} \lim_{t \rightarrow \infty} v(x,t) = \frac{1}{D_1 D_2} \left\{ \frac{C(0)}{y_1^{1/2}(0)} \exp \left[ -y_1^{1/2}(0) x \right] \right. \\ \left. + \frac{E(0)}{y_2^{1/2}(0)} \exp \left[ -y_2^{1/2}(0) x \right] \right\} \quad (6.5.8) \end{aligned}$$

where  $y_1(0), y_2(0)$  are values of  $y_1(p), y_2(p)$  for  $p = 0$  and  $A(0), B(0), C(0), E(0)$  are obtained by putting  $p = 0$  in the corresponding expressions (6.5.3).

It can be verified that the expressions (6.5.7) and (6.5.8) satisfy the steady state form of the system (6.2.8)

with boundary conditions (6.2.10). Thus it is seen that the nonstationary solutions tend to the corresponding stationary solutions as  $t \rightarrow \infty$ , showing the asymptotic stability of the equilibrium state under flux boundary conditions for  $eh > fg$ . It is also observed from (6.5.7) and (6.5.8) that spatial pattern is formed by steady state solutions.

#### Case (ii) Reservoir conditions

In this case, on solving the system (6.2.8) for  $\mu_1 = \mu_2 = 0$  with conditions (6.2.11), we obtain

$$\begin{aligned} \bar{u}(x,p) = & \frac{1}{D_1 D_2 p} \{ A'(p) \exp [-y_1^{1/2}(p) x] \\ & + B'(p) \exp [-y_2^{1/2}(p) x] \} \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp [-y_1^{1/2}(p) z]}{y_1^{1/2}(p)} [F_1(p, z+x) - F_1(p, z-x)] \right. \\ & \left. + \frac{\exp [-y_2^{1/2}(p) z]}{y_2^{1/2}(p)} [F_2(p, z+x) - F_2(p, z-x)] \right\} dz \quad (6.5.9) \end{aligned}$$

$$\begin{aligned} \bar{v}(x,p) = & \frac{1}{D_1 D_2 p} \{ C'(p) \exp [-y_1^{1/2}(p) x] \\ & + E'(p) \exp [-y_2^{1/2}(p) x] \} \\ & + \frac{1}{2D_1 D_2} \int_0^\infty \left\{ \frac{\exp [-y_1^{1/2}(p) z]}{y_1^{1/2}(p)} [G_1(p, z+x) - G_1(p, z-x)] \right. \\ & \left. + \frac{\exp [-y_2^{1/2}(p) z]}{y_2^{1/2}(p)} [G_2(p, z+x) - G_2(p, z-x)] \right\} dz \quad (6.5.10) \end{aligned}$$

where  $\bar{u}(x,p)$ ,  $\bar{v}(x,p)$  are Laplace transforms of  $u(x,t)$ ,  $v(x,t)$  respectively and

$$\begin{aligned} A'(p) &= \frac{(D_2 y_1 - p - h) D_1 U_1 + f D_2 V_1}{y_1 - y_2} \\ B'(p) &= \frac{(p + h - D_2 y_2) D_1 U_1 - f D_2 V_1}{y_1 - y_2} \\ C'(p) &= \frac{(D_1 y_1 - p - e) D_2 V_1 + g D_1 U_1}{y_1 - y_2} \\ E'(p) &= \frac{(p + e - D_1 y_2) D_2 V_1 - g D_1 U_1}{y_1 - y_2}. \end{aligned} \quad (6.5.11)$$

To investigate the asymptotic behavior of  $u(x,t)$  and  $v(x,t)$  as  $t \rightarrow \infty$ , using (6.5.6) in (6.5.9) and (6.5.10), we get

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x,t) &= \frac{1}{D_1 D_2} \{ A'(0) \exp [-y_1^{1/2}(0) x] \\ &\quad + B'(0) \exp [-y_2^{1/2}(0) x] \} \end{aligned} \quad (6.5.12)$$

$$\begin{aligned} \lim_{t \rightarrow \infty} v(x,t) &= \frac{1}{D_1 D_2} \{ C'(0) \exp [-y_1^{1/2}(0) x] \\ &\quad + E'(0) \exp [-y_2^{1/2}(0) x] \} \end{aligned} \quad (6.5.13)$$

where  $A'(0)$ ,  $B'(0)$ ,  $C'(0)$ ,  $E'(0)$  are obtained by putting  $p = 0$  in the corresponding expressions (6.5.11).

Since the expressions given by (6.5.12) and (6.5.13) satisfy the steady state form of the system (6.2.8) with

reservoir conditions (6.2.11), the asymptotic stability of the equilibrium state is established in this case also provided  $eh > fg$ . It can also be seen that the steady state solutions give rise to spatial pattern due to nonhomogeneous boundary conditions.

Thus it is concluded that an otherwise stable equilibrium state without dispersal remains so with dispersal in the case of infinite habitat.

#### 6.6 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL UNDER RESERVOIR CONDITIONS

To investigate the effect of convective migration on the linear stability of the equilibrium state of the system (6.2.8) under reservoir conditions (6.2.11), consider the case for which

$$\frac{\mu_1}{D_1} = \frac{\mu_2}{D_2} \quad (6.6.1)$$

i.e. the ratio of convective velocity to dispersal coefficient is same for both species. This is biologically reasonable because the species having more dispersal ability are likely to have faster convective migration velocity.

Using the transformations

$$\begin{aligned} u(x,t) &= \exp(\mu_1 x / 2D_1) u_1(x,t) \\ v(x,t) &= \exp(\mu_2 x / 2D_2) v_1(x,t) \end{aligned} \quad (6.6.2)$$

the system (6.2.8) is reduced to the following form

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= -e_1 u_1 - f v_1 + D_1 \frac{\partial^2 u_1}{\partial x^2} \\ \frac{\partial v_1}{\partial t} &= -g u_1 - h_1 v_1 + D_2 \frac{\partial^2 v_1}{\partial x^2}\end{aligned}\tag{6.6.3}$$

where

$$e_1 = e + \mu_1^2/4D_1 ; \quad h_1 = h + \mu_2^2/4D_2.\tag{6.6.4}$$

The initial and boundary conditions (6.2.11) are modified as follows:

$$\begin{aligned}u_1(x,0) &= r_1(x), \quad v_1(x,0) = s_1(x) \quad x > 0 \\ u_1(0,t) &= U_1, \quad v_1(0,t) = V_1 \quad t \geq 0 \\ u_1(x,t) &\rightarrow 0, \quad v_1(x,t) \rightarrow 0\end{aligned}\tag{6.6.5}$$

are  $x \rightarrow L$  for finite habitat or  $x \rightarrow \infty$  for infinite habitat. The functions  $r_1(x)$  and  $s_1(x)$  are given by

$$\begin{aligned}r_1(x) &= r(x) \exp(-\mu_1 x/2D_1) \\ s_1(x) &= s(x) \exp(-\mu_2 x/2D_2) .\end{aligned}\tag{6.6.6}$$

It is noted that the system (6.6.3) with conditions (6.6.5) is of the same form as that of the system (6.2.8) for  $\mu_1 = \mu_2 = 0$  with conditions (6.2.11) where  $e_1, h_1, r_1(x), s_1(x)$  have been modified according to (6.6.4) and (6.6.6). Therefore, the solutions of the system (6.2.8) with (6.6.1) are obtained from case (ii) of Sections 6.4 and 6.5 by making use of (6.6.2), (6.6.4) and (6.6.5) appropriately.

For example, in the case of finite habitat, the solutions of the system (6.2.8) with conditions (6.2.11) for the case of (6.6.1) can be obtained from (6.4.11) and (6.4.12) by multiplying these equations with  $\exp(u_1 x / 2D_1)$  and  $\exp(u_2 x / 2D_2)$  respectively and replacing  $e$  by  $e_1$ ,  $h$  by  $h_1$ ,  $r(x)$  by  $r_1(x)$ ,  $s(x)$  by  $s_1(x)$ . Thus the corresponding eigen values  $p'_{1n}$ ,  $p'_{2n}$  ( $n=1,2,3,\dots$ ) for the system (6.6.3) with (6.6.2) are given by

$$\begin{pmatrix} p'_{1n} \\ p'_{2n} \end{pmatrix} = \frac{1}{2} \left( \frac{n^2 \pi^2}{L^2} D_1 + \frac{n^2 \pi^2}{L^2} D_2 + e_1 + h_1 \right) \pm \frac{1}{2} \left[ \left( \frac{n^2 \pi^2}{L^2} D_1 - \frac{n^2 \pi^2}{L^2} D_2 + e_1 - h_1 \right)^2 + 4fg \right]^{1/2}. \quad (6.6.7)$$

It is seen from (6.6.7) that  $p'_{1n}$ ,  $p'_{2n}$  ( $n=1,2,3,\dots$ ) are positive provided

$$\left( \frac{\pi^2}{L^2} D_1 + \frac{u_1^2}{4D_1} + e \right) \left( \frac{\pi^2}{L^2} D_2 + \frac{u_2^2}{4D_2} + h \right) > fg. \quad (6.6.8)$$

It has also been shown that (see appendix, Chapter IV)  $p'_{1n}$ ,  $p'_{2n}$  ( $n=1,2,3,\dots$ ) increase with  $u_1$  and  $u_2$ .

Keeping in view the conditions (6.4.6) and (6.6.8), it is concluded that even an otherwise unstable equilibrium state with dispersal can become stable due to convective migration and the degree of stability increases with convective velocities.

## 6.7 STABILITY ANALYSIS WITH CONVECTION AND DISPERSAL IN A TWO DIMENSIONAL FINITE HABITAT UNDER RESERVOIR CONDITIONS

Though we considered the migration of the species only along x-direction in the earlier sections, in real situations, migration takes place in all possible directions. In such cases, the equations governing their evolution in rectangular habitats  $[L, M]$  being the lengths of the habitat along x, y-directions respectively] are written as

$$\frac{\partial N_1}{\partial t} + u_1 \frac{\partial N_1}{\partial x} + u_3 \frac{\partial N_1}{\partial y} = N_1 \left( a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1 + \alpha N_1} \right) + D_1 \frac{\partial^2 N_1}{\partial x^2} + D_3 \frac{\partial^2 N_1}{\partial y^2} \quad (6.7.1)$$

$$\frac{\partial N_2}{\partial t} + u_2 \frac{\partial N_2}{\partial x} + u_4 \frac{\partial N_2}{\partial y} = N_2 \left( a_2 - a_{22}N_2 - \frac{a_{21}N_1}{1 + \alpha N_1} \right) + D_2 \frac{\partial^2 N_2}{\partial x^2} + D_4 \frac{\partial^2 N_2}{\partial y^2}$$

where  $D_1, D_2, D_3, D_4$  are co-efficients of dispersal of the species and  $u_1, u_2, u_3, u_4$  their convective velocities.

Analogous to Section 6.6, consider the case

$$\frac{u_1}{D_1} = \frac{u_2}{D_2} ; \frac{u_3}{D_3} = \frac{u_4}{D_4} \quad (6.7.2)$$

i.e. the ratio of convective velocity to dispersal co-efficient is same for both the species along the particular direction. Analysing as before, it may be observed that the equilibrium state is asymptotically stable under reservoir conditions provided



$$\left(\frac{\pi^2}{L^2} D_1 + \frac{\pi^2}{M^2} D_3 + \frac{u_1^2}{4D_1} + \frac{u_3^2}{4D_3}\right) \left(\frac{\pi^2}{L^2} D_2 + \frac{\pi^2}{M^2} D_4 + \frac{u_2^2}{4D_2} + \frac{u_4^2}{4D_4}\right) > fg. \quad (6.7.3)$$

Comparing (6.7.3) with the condition (6.6.8), it is concluded that the equilibrium state which is unstable in one dimensional finite habitat may become stable in two dimensional finite habitat due to convective and dispersive migration.

## 6.8 CONCLUSION

Effects of convective and dispersive migration on the linear stability of the equilibrium state for two competing species system with intraspecific interactions and functional response have been examined. It has been shown that the functional response has destabilizing effect. In both finite and semi-infinite habitats, it has also been shown that the stable equilibrium state without dispersal remains so with dispersal under flux and reservoir conditions. In all these cases, it has been pointed out that the steady state populations form spatial pattern due to nonhomogeneous boundary conditions.

In the case of finite habitat, it has been noticed that the degree of stability increases with dispersal co-efficients in absence of convective migration and dispersal may stabilize even an otherwise unstable equilibrium state without migration under reservoir conditions. It has also been pointed out that

the effect of convective migration of the species is to stabilize even an otherwise unstable equilibrium state with dispersal and the degree of stability increases with convective velocities. It has been noted that the equilibrium state which is unstable in one dimensional finite habitat may become stable in two dimensional finite habitat under reservoir conditions.

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## CHAPTER VII

### EFFECTS OF DISPERSAL ON THE LINEAR STABILITY OF PREY-PREDATOR SYSTEM WITH FUNCTIONAL RESPONSE IN A CIRCULAR FINITE HABITAT

#### 7.1 INTRODUCTION

In Chapter V, effects of convective and dispersive migration on the linear stability of the equilibrium state for prey-predator system with functional response have been examined in one and two dimensional linear habitats. As a continuation, in the present chapter, similar study is conducted on prey-predator interactions with dispersal in a circular finite habitat.

Extensive research has been done on the evolution and co-existence of interacting species by considering temporal variations of the species, Holling [3], Kazarinoff and Driessche [4], Lin and Kahn [7], Rapport and Turner [9]. It should, however, be noted that the effects of dispersal on the stability of the equilibrium state of systems of interacting species have also been investigated, Comins and Blatt [1], Haderler et al. [2], Leung [5], Levin [6], Murtrie [8], Segel and Levin [10], Skellam [11]. In particular, Comins and Blatt [1] have pointed out that dispersal can lead to stability and continued co-existence of the species. It may also be noted here that the equilibrium state of systems of

interacting species with functional response are not always stable (Kazarinoff and Driessche [4], Lin and Kahn [7]) and the effects of dispersal on the stability of such systems have not been investigated.

Keeping all these in view, in the following, we investigate the effects of dispersal on the linear stability of the equilibrium state for prey-predator system in a circular habitat by considering intraspecific interactions and functional response.

## 7.2 BASIC EQUATIONS

Consider the evolution of two interacting and dispersing species forming a prey-predator system in a circular ( $0 \leq r \leq R$ ) habitat. By taking into account the effects of functional response, the equations governing the evolution of the species can be written as,

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1(a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1}) + D_1 \frac{1}{r} \frac{\partial}{\partial r} (r \frac{\partial N_1}{\partial r}) \\ \frac{\partial N_2}{\partial t} &= N_2(-a_2 + \frac{a_{21}N_1}{1+\alpha N_1}) + D_2 \frac{1}{r} \frac{\partial}{\partial r} (r \frac{\partial N_2}{\partial r})\end{aligned}\tag{7.2.1}$$

where  $N_1(r,t)$ ,  $N_2(r,t)$  represent the population distributions of prey and predator species respectively at time  $t$ ;  $D_1$ ,  $D_2$  are the co-efficients of dispersal; and the interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, \alpha$  are positive constants. The term

$(1 + \alpha N_1)^{-1}$  characterizes the functional response in the system and  $\alpha$  determines its strength.

The nontrivial equilibrium state  $(N_1^*, N_2^*)$  of the system (7.2.1) is given by

$$N_1^* = \frac{a_2}{a_{21} - a_2 \alpha} ; N_2^* = \frac{a_{21}}{a_{12}} \frac{[a_1(a_{21} - a_2 \alpha) - a_2 a_{11}]}{(a_{21} - a_2 \alpha)^2} . \quad (7.2.2)$$

It is noted from (7.2.2) that both  $N_1^*$  and  $N_2^*$  are positive provided

$$a_1(a_{21} - a_2 \alpha) > a_2 a_{11} . \quad (7.2.3)$$

To examine the local stability of the equilibrium state  $(N_1^*, N_2^*)$ , we linearise the system (7.2.1) by writing

$$\begin{aligned} N_1(r, t) &= N_1^* + u(r, t) \\ N_2(r, t) &= N_2^* + v(r, t) \end{aligned} \quad (7.2.4)$$

which on substituting in the system (7.2.1) and using (7.2.2) gives

$$\begin{aligned} \frac{\partial u}{\partial t} &= -eu - fv + D_1 \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial u}{\partial r} \right) \\ \frac{\partial v}{\partial t} &= gu + D_2 \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial v}{\partial r} \right) \end{aligned} \quad (7.2.5)$$

where

$$\begin{aligned} e &= \frac{N_1^*}{(1 + \alpha N_1^*)} \frac{[a_{11}(a_{21} + a_2 \alpha) - a_1 \alpha(a_{21} - a_2 \alpha)]}{(a_{21} - a_2 \alpha)} \\ f &= \frac{a_{12} N_1^*}{(1 + \alpha N_1^*)} ; g = \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2} . \end{aligned} \quad (7.2.6)$$

From (7.2.6), it may be noted that  $f$  and  $g$  are positive under (7.2.3). The constant  $e$  is positive for  $a_{11} > a_0$  and negative for  $a_{11} < a_0$  where

$$a_0 = a_1 \alpha \frac{(a_{21} - a_2 \alpha)}{(a_{21} + a_2 \alpha)} \geq 0. \quad (7.2.7)$$

It should be here noted that the equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable in absence of dispersal (refer Chapter V) for  $\alpha \geq 0$  provided

$$e > 0. \quad (7.2.8)$$

The following initial and boundary conditions are associated with the system (7.2.5).

(i) Reservoir conditions

$$\begin{aligned} u(r, 0) &= u_0(r), \quad v(r, 0) = v_0(r) & 0 \leq r < R \\ u(R, t) &= U_1, \quad v(R, t) = V_1 & t \geq 0 \\ u(r, t) \text{ and } v(r, t) &\text{ are finite at } r = 0. \end{aligned} \quad (7.2.9)$$

In physical situations, this kind of problem arises when the population density of the dispersive species is prescribed at the boundary.

(ii) Efflux conditions

$$\begin{aligned} u(r, 0) &= u_0(r), \quad v(r, 0) = v_0(r) & 0 \leq r < R \\ \frac{\partial u}{\partial r} + ku &= U_2, \quad \frac{\partial v}{\partial r} + kv = V_2 & t \geq 0 \\ & & \text{at } r = R \\ u(r, t) \text{ and } v(r, t) &\text{ are finite at } r = 0. \end{aligned} \quad (7.2.10)$$

The boundary conditions (7.2.10) indicate that the flux of the population density at the periphery of the circular habitat depends upon density of the population at the boundary.

In the following, the linear stability of the equilibrium state  $(N_1^*, N_2^*)$  is studied under (7.2.3).

### 7.3 STABILITY ANALYSIS WITH DISPERSAL UNDER RESERVOIR CONDITIONS

By using Laplace and finite Hankel transforms, the system (7.2.5) is solved with conditions (7.2.9) in a circular habitat  $(0 \leq r \leq R)$  to obtain  $u(r, t)$  and  $v(r, t)$  as

$$\begin{aligned}
 u(r, t) = & \frac{2}{R} \sum_n x_n \frac{J_0(r x_n)}{J_1(R x_n)} \int_0^t \left[ A_n \exp(-p_{1n} T) \right. \\
 & \left. + B_n \exp(-p_{2n} T) \right] dT \\
 & + \frac{2}{R^2} \sum_n \frac{J_0(r x_n)}{[J_1(R x_n)]^2} \left[ F_{1n} \exp(-p_{1n} t) \right. \\
 & \left. + F_{2n} \exp(-p_{2n} t) \right] \quad (7.3.1)
 \end{aligned}$$

$$\begin{aligned}
 v(r, t) = & \frac{2}{R} \sum_n x_n \frac{J_0(r x_n)}{J_1(R x_n)} \int_0^t \left[ C_n \exp(-p_{1n} T) \right. \\
 & \left. + E_n \exp(-p_{2n} T) \right] dT \\
 & + \frac{2}{R^2} \sum_n \frac{J_0(r x_n)}{[J_1(R x_n)]^2} \left[ G_{1n} \exp(-p_{1n} t) \right. \\
 & \left. + G_{2n} \exp(-p_{2n} t) \right] \quad (7.3.2)
 \end{aligned}$$

where  $J_m(x)$  is Bessel function of order  $m$  and the summation



is taken over all the positive roots,  $x_n$ , of the transcendental equation

$$J_0(R x) = 0. \quad (7.3.3)$$

The constant co-efficients in (7.3.1) and (7.3.2) are defined as follows:

$$\begin{aligned} A_n &= \frac{D_1(p_{1n} - D_2 x_n^2) U_1 + f D_2 V_1}{p_{1n} - p_{2n}} \\ B_n &= \frac{D_1(D_2 x_n^2 - p_{2n}) U_1 - f D_2 V_1}{p_{1n} - p_{2n}} \\ C_n &= \frac{D_2(p_{1n} - D_1 x_n^2 - e) V_1 - g D_1 U_1}{p_{1n} - p_{2n}} \\ E_n &= \frac{D_2(D_1 x_n^2 + e - p_{2n}) V_1 + g D_1 U_1}{p_{1n} - p_{2n}} \\ F_{1n} &= \frac{(p_{1n} - D_2 x_n^2) u_{on} + f v_{on}}{p_{1n} - p_{2n}} \\ F_{2n} &= \frac{(D_2 x_n^2 - p_{2n}) u_{on} - f v_{on}}{p_{1n} - p_{2n}} \\ G_{1n} &= \frac{(p_{1n} - D_1 x_n^2 - e) v_{on} - g u_{on}}{p_{1n} - p_{2n}} \\ G_{2n} &= \frac{(D_1 x_n^2 + e - p_{2n}) v_{on} + g u_{on}}{p_{1n} - p_{2n}} \end{aligned} \quad (7.3.4)$$

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} (D_1 x_n^2 + D_2 x_n^2 + e) \pm \frac{1}{2} [(D_1 x_n^2 - D_2 x_n^2 + e)^2 - 4fg]^{1/2} \quad (7.3.5)$$

$$(7.3.6)$$

where  $u_{on}$  and  $v_{on}$  are finite Hankel transforms of the first kind defined as

$$u_{on} = \int_0^R r u_o(r) J_o(r x_n) dr$$

$$v_{on} = \int_0^R r v_o(r) J_o(r x_n) dr.$$
(7.3.7)

From (7.3.6) it may be noted that  $p_{1n}$  and  $p_{2n}$  or their real parts are positive for all values of  $n$  if

$$\min_n (D_1 x_n^2 + e) \geq 0.$$
(7.3.8)

It is also seen that  $p_{1n}$  and  $p_{2n}$  or their real parts increase with dispersal co-efficients for fixed  $(D_1 - D_2)$ .

If the inequality (7.3.8) holds, i.e.  $p_{1n}, p_{2n} (n = 1, 2, 3, \dots)$  or their real parts are positive,  $u(r, t)$  and  $v(r, t)$  given by (7.3.1) and (7.3.2) take the following forms as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(r, t) = \frac{2}{R} \sum_n x_n \frac{J_o(r x_n)}{J_1(R x_n)} \left[ \frac{A_n}{p_{1n}} + \frac{B_n}{p_{2n}} \right]$$
(7.3.9)

$$\lim_{t \rightarrow \infty} v(r, t) = \frac{2}{R} \sum_n x_n \frac{J_o(r x_n)}{J_1(R x_n)} \left[ \frac{C_n}{p_{1n}} + \frac{E_n}{p_{2n}} \right].$$
(7.3.10)

It can be easily verified that the expressions (7.3.9) and (7.3.10) represent the steady state solutions of the system (7.2.5) with boundary conditions (7.2.9). Since the nonstationary solutions (7.3.1) and (7.3.2) tend to the corresponding stationary solutions (7.3.9) and (7.3.10) as

$t \rightarrow \infty$ , the equilibrium state is asymptotically stable under (7.3.8). It may also be pointed out that the degree of stability of the equilibrium state increases with dispersal co-efficients provided  $(D_1 - D_2)$  is fixed.

Keeping in view of the condition (7.3.8), the following conclusions can also be drawn :

- (i) When  $e = 0$ , the equilibrium state is asymptotically stable. Hence dispersal stabilizes an otherwise neutrally stable equilibrium state.
- (ii) When  $e > 0$ , the equilibrium state is stable. Hence the stable equilibrium state without dispersal remains stable with dispersal.
- (iii) When  $e < 0$  i.e.  $a_{11} < a_0$ , the equilibrium state is stable if (7.3.8) is satisfied.

Finally, if (7.3.8) does not hold, then there exists least one positive value of  $n$ , say  $n = n_0$ , for which  $p_{2n}$  is negative and in that case the equilibrium state is unstable.

#### 7.4 STABILITY ANALYSIS WITH DISPERSAL UNDER EFFLUX CONDITIONS

As before, on solving the system (7.2.5) with conditions (7.2.10) in a circular habitat ( $0 \leq r \leq R$ ),  $u(r,t)$  and  $v(r,t)$  are obtained as

$$\begin{aligned}
u(r,t) = & \frac{2}{R} \sum_n I_n(r) \int_0^t \left[ A'_n \exp(-p'_{1n} T) + B'_n \exp(-p'_{2n} T) \right] dT \\
& + \frac{2}{R^2} \sum_n \frac{I_n(r)}{J_0(R y_n)} \left[ F'_{1n} \exp(-p'_{1n} t) \right. \\
& \quad \left. + F'_{2n} \exp(-p'_{2n} t) \right] \quad (7.4.1)
\end{aligned}$$

$$\begin{aligned}
v(r,t) = & \frac{2}{R} \sum_n I_n(r) \int_0^t \left[ C'_n \exp(-p'_{1n} T) + E'_n \exp(-p'_{2n} T) \right] dT \\
& + \frac{2}{R^2} \sum_n \frac{I_n(r)}{J_0(R y_n)} \left[ G'_{1n} \exp(-p'_{1n} t) \right. \\
& \quad \left. + G'_{2n} \exp(-p'_{2n} t) \right] \quad (7.4.2)
\end{aligned}$$

where the summation is taken over all positive roots,  $y_n$ , of the transcendental equation

$$k J_0(R y) = y J_1(R y). \quad (7.4.3)$$

The function  $I_n(r)$  is defined as

$$I_n(r) = \frac{J_0(r y_n)}{J_0(R y_n)} \frac{y_n^2}{(k^2 + y_n^2)}. \quad (7.4.4)$$

The constant co-efficients in (7.4.1) and (7.4.2) are given as follows :

$$\begin{aligned}
 A'_n &= \frac{D_1(p'_{1n} - D_2 y_n^2) U_2 + f D_2 V_2}{p'_{1n} - p'_{2n}} \\
 B'_n &= \frac{D_1(D_2 y_n^2 - p'_{2n}) U_2 - f D_2 V_2}{p'_{1n} - p'_{2n}} \\
 C'_n &= \frac{(p'_{1n} - D_1 y_n^2 - e) D_2 V_2 - g D_1 U_2}{p'_{1n} - p'_{2n}} \\
 E'_n &= \frac{(D_1 y_n^2 + e - p'_{2n}) D_2 V_2 + g D_1 U_2}{p'_{1n} - p'_{2n}} \quad (7.4.5)
 \end{aligned}$$

$$\begin{aligned}
 F'_{1n} &= \frac{(p'_{1n} - D_2 y_n^2) u'_{on} + f v'_{on}}{p'_{1n} - p'_{2n}} \\
 F'_{2n} &= \frac{(D_2 y_n^2 - p'_{2n}) u'_{on} - f v'_{on}}{p'_{1n} - p'_{2n}} \\
 G'_{1n} &= \frac{(p'_{1n} - D_1 y_n^2 - e) v'_{on} - g u'_{on}}{p'_{1n} - p'_{2n}} \\
 G'_{2n} &= \frac{(D_1 y_n^2 + e - p'_{2n}) v'_{on} + g u'_{on}}{p'_{1n} - p'_{2n}} \quad (7.4.6)
 \end{aligned}$$

$$\begin{pmatrix} p'_{1n} \\ p'_{2n} \end{pmatrix} = \frac{1}{2} (D_1 y_n^2 + D_2 y_n^2 + e) \pm \frac{1}{2} [(D_1 y_n^2 - D_2 y_n^2 + e)^2 - 4fg]^{\frac{1}{2}} \quad (7.4.7)$$

where  $u'_{on}$ ,  $v'_{on}$  are

$$u'_{on} = \int_0^R r u_o(r) J_o(r y_n) dr$$

$$v'_{on} = \int_0^R r v_o(r) J_o(r y_n) dr.$$
(7.4.8)

From (7.4.7), it may be noted that  $p'_{1n}$ ,  $p'_{2n}$  or their real parts are positive for all values of  $n$  provided

$$\min_n (D_1 y_n^2 + e) \geq 0.$$
(7.4.9)

If (7.4.9) does not hold, then there may exist least positive value of  $n$ , say  $n = n_o$ , for which  $p'_{2n}$  is negative.

If (7.4.9) is satisfied i.e.  $p'_{1n}$ ,  $p'_{2n}$  or their real parts are positive for all values of  $n$ ,  $u(r,t)$  and  $v(r,t)$  given by (7.4.1) and (7.4.2) respectively converge to the following forms as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(r,t) = \frac{2}{R} \sum_n I_n(r) \left[ \frac{A'_n}{p'_{1n}} + \frac{B'_n}{p'_{2n}} \right]$$
(7.4.10)

$$\lim_{t \rightarrow \infty} v(r,t) = \frac{2}{R} \sum_n I_n(r) \left[ \frac{C'_n}{p'_{1n}} + \frac{E'_n}{p'_{2n}} \right].$$
(7.4.11)

As the expressions (7.4.10) and (7.4.11) satisfy the steady state form of the system (7.2.5) with boundary conditions (7.2.10), the equilibrium state is asymptotically stable under (7.4.9). It may also be noted that the degree of stability of

the equilibrium state increases with dispersal co-efficients for fixed  $(D_1 - D_2)$ .

Keeping in view of the inequality (7.4.9), the following conclusions are also noted :

- (i) When  $e = 0$ , the equilibrium state is asymptotically stable. Hence dispersal has the effect to stabilize an otherwise neutrally stable equilibrium state.
- (ii) When  $e > 0$ , the equilibrium state is always stable. Hence dispersal stabilizes further the already stable equilibrium state without dispersal.
- (iii) When  $e < 0$ , the equilibrium state is asymptotically stable provided (7.4.9) is satisfied. If the inequality (7.4.9) does not hold, the equilibrium state may be unstable.

## 7.5 CONCLUSION

In a circular habitat, effects of dispersal on the linear stability of the equilibrium state for prey-predator system with intraspecific interactions and functional response have been investigated. Both under reservoir and efflux boundary conditions, it has been shown that the equilibrium state is asymptotically stable for  $e \geq 0$ . Thus it is concluded that the equilibrium state which is stable without dispersal remains so with dispersal. However, it has also been pointed out that even an otherwise unstable equilibrium state can

become stable with dispersal provided certain inequalities such as (7.3.8), (7.4.9) involving dispersal co-efficients hold. It has also been observed that the degree of stability of the equilibrium state increases with dispersal co-efficients if their difference is fixed.



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## CHAPTER VIII

### EFFECTS OF DISPERSAL ON THE LINEAR STABILITY OF TWO COMPETING SPECIES SYSTEM IN A CIRCULAR FINITE HABITAT

#### 8.1 INTRODUCTION

The linear stability of the equilibrium state of system of two competing species with functional response have been studied in Chapter VI by considering the effects of convective and dispersive migration of the species. In the current chapter, similar analysis is carried out on dispersive competitive species in a circular habitat.

Since the days of Volterra, the evolution and co-existence of interacting species have been studied by ignoring the effects of migration, Brauer [1], Gomatham and Mac Donald [2], Leou and Tumpson [6], Lin and Kahm [8]. The effects of dispersal on the dynamics of biological species have also been investigated more extensively, Gopalsamy [3], Haderler et al. [4], Harada and Fukao [5], Levin [7], Segel and Levin [9], Skellam [10]. In particular, Haderler et al. [4] have examined the effect of boundary conditions on the dynamics of dispersive prey-predator species in a linear habitat. Similar analysis has also been carried out by Gopalsamy [3] on the dynamics of two competing and dispersive

species in a linear habitat and found that reservoir type boundary conditions lead to stable co-existence only if a delicate relation on the boundary holds. Harada and Fukao [5] have also investigated the co-existence of two competing species over a linear habitat of finite length by considering the nonlinear effect.

Keeping the above in view, in the following, we investigate the effects of dispersal on the linear stability of the equilibrium state of two competing species system with intraspecific interactions and functional response (Lin and Kahn [8]) in a circular habitat.

## 8.2 BASIC EQUATIONS

Consider the evolution of two competing and dispersing species with intraspecific interactions and functional response in a circular ( $0 \leq r \leq R$ ) habitat. The evolution of the species in such a habitat is described by the following system of dynamical equations (Lin and Kahn [8], Skellam [10])

$$\frac{\partial N_1}{\partial t} = N_1(a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1}) + D_1 \frac{1}{r} \frac{\partial}{\partial r} (r \frac{\partial N_1}{\partial r}) \quad (8.2.1)$$

$$\frac{\partial N_2}{\partial t} = N_2(a_2 - a_{22}N_2 - \frac{a_{21}N_1}{1+\alpha N_1}) + D_2 \frac{1}{r} \frac{\partial}{\partial r} (r \frac{\partial N_2}{\partial r})$$

where  $N_1(r, t)$ ,  $N_2(r, t)$  represent the population distributions of two species at time  $t$ ;  $D_1$ ,  $D_2$  are the co-efficients of

dispersal. The interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, a_{22}$  and  $\alpha$  are positive constants. The term  $(1 + \alpha N_1)^{-1}$  which arises due to the functional response in the model is characterized by  $\alpha$ .

The nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (8.2.1) is obtained from

$$\begin{aligned} a_1 - a_{11}N_1^* - \frac{a_{12}N_2^*}{1 + \alpha N_1^*} &= 0 \\ a_2 - a_{22}N_2^* - \frac{a_{21}N_1^*}{1 + \alpha N_1^*} &= 0 \end{aligned} \quad (8.2.2)$$

It has been verified from (8.2.2) that there exists only one positive value for  $N_1^*$  and  $N_2^*$  under the following conditions (see Chapter VI)

$$\frac{a_{22}}{a_{12}} > \frac{a_2}{a_1} > \frac{a_{21}}{a_{11}} \quad (8.2.3)$$

$$\text{and } a_{21} > a_2 \alpha \quad (8.2.4)$$

The system (8.2.1) is linearised to study the local stability of the equilibrium state  $(N_1^*, N_2^*)$  by writing

$$\begin{aligned} N_1(r, t) &= N_1^* + u(r, t) \\ N_2(r, t) &= N_2^* + v(r, t) \end{aligned} \quad (8.2.5)$$

which on substituting in (8.2.1) and making use of (8.2.2) gives

$$\begin{aligned}\frac{\partial u}{\partial t} &= -eu - fv + D_1 \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial u}{\partial r} \right) \\ \frac{\partial v}{\partial t} &= -gu - hv + D_2 \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial v}{\partial r} \right)\end{aligned}\tag{8.2.6}$$

where  $u, v$  are perturbed population distributions and

$$\begin{aligned}e &= \frac{N_1^*}{(1 + \alpha N_1^*)} (a_{11} - a_1 \alpha + 2a_{11} \alpha N_1^*) \\ f &= \frac{a_{12} N_1^*}{(1 + \alpha N_1^*)} \\ g &= \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2} ; \quad h = a_{22} N_2^*\end{aligned}\tag{8.2.7}$$

which are positive in view of (8.2.3) and (8.2.4).

If the species are nondispersive, it has been shown that the nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable for  $\alpha \geq 0$  (see Chapter VI) provided

$$eh > fg.\tag{8.2.8}$$

In the forthcoming sections, the stability of the equilibrium state  $(N_1^*, N_2^*)$  of the system (8.2.1) is analysed by associating the linearised system (8.2.6) with the following initial and boundary conditions.

(i) Reservoir conditions

$$\begin{aligned}u(r, 0) &= u_0(r), \quad v(r, 0) = v_0(r) \quad 0 \leq r < R \\ u(R, t) &= U_1, \quad v(R, t) = V_1 \quad t \geq 0 \\ u(r, t) \text{ and } v(r, t) &\text{ are finite at } r=0.\end{aligned}\tag{8.2.9}$$

(ii) Efflux conditions

$$u(r,0) = u_0(r), \quad v(r,0) = v_0(r) \quad 0 \leq r < R$$

$$\frac{\partial u}{\partial r} + ku = U_2, \quad \frac{\partial v}{\partial r} + kv = V_2 \quad \text{at } r = R \quad (8.2.10)$$

$u(r,t)$  and  $v(r,t)$  are finite at  $r=0$ .

### 8.3 STABILITY ANALYSIS WITH DISPERSAL UNDER RESERVOIR CONDITIONS

In this case, on solving the system (8.2.6) with conditions (8.2.9) in a circular habitat ( $0 \leq r \leq R$ ) by using Laplace and finite Hankel transforms, we obtain  $u(r,t)$  and  $v(r,t)$  as

$$\begin{aligned} u(r,t) = & \frac{2}{R} \sum_n \frac{x_n J_0(rx_n)}{J_1(Rx_n)} \int_0^t [A_n \exp(-p_{1n}T) + B_n \exp(-p_{2n}T)] dT \\ & + \frac{2}{R^2} \sum_n \frac{J_0(rx_n)}{[J_1(Rx_n)]^2} [F_{1n} \exp(-p_{1n}t) + F_{2n} \exp(-p_{2n}t)] \end{aligned} \quad (8.3.1)$$

$$\begin{aligned} v(r,t) = & \frac{2}{R} \sum_n x_n \frac{J_0(rx_n)}{J_1(Rx_n)} \int_0^t [C_n \exp(-p_{1n}T) + E_n \exp(-p_{2n}T)] dT \\ & + \frac{2}{R^2} \sum_n \frac{J_0(rx_n)}{[J_1(Rx_n)]^2} [G_{1n} \exp(-p_{1n}t) + G_{2n} \exp(-p_{2n}t)] \end{aligned} \quad (8.3.2)$$

where  $J_m(x)$  is the Bessel function of order  $m$  and the summation is taken over all positive roots,  $x_n$ , of the transcendental equation

$$J_0(Rx) = 0. \quad (8.3.3)$$

The constant coefficients used in (8.3.1) and (8.3.2) are given by

$$\begin{aligned}
 A_n &= \frac{D_1(p_{1n} - D_2 x_n^2 - h)U_1 + f D_2 V_1}{p_{1n} - p_{2n}} \\
 B_n &= \frac{D_1(D_2 x_n^2 + h - p_{2n})U_1 - f D_2 V_1}{p_{1n} - p_{2n}} \\
 C_n &= \frac{D_2(p_{1n} - D_1 x_n^2 - e)V_1 + g D_1 U_1}{p_{1n} - p_{2n}} \\
 E_n &= \frac{D_2(D_1 x_n^2 + e - p_{2n})V_1 - g D_1 U_1}{p_{1n} - p_{2n}}
 \end{aligned} \tag{8.3.4}$$

$$\begin{aligned}
 F_{1n} &= \frac{(p_{1n} - D_2 x_n^2 - h)u_{on} + f v_{on}}{p_{1n} - p_{2n}} \\
 F_{2n} &= \frac{(D_2 x_n^2 + h - p_{2n})u_{on} - f v_{on}}{p_{1n} - p_{2n}} \\
 G_{1n} &= \frac{(p_{1n} - D_1 x_n^2 - e)v_{on} + g u_{on}}{p_{1n} - p_{2n}} \\
 G_{2n} &= \frac{(D_1 x_n^2 + e - p_{2n})v_{on} - g u_{on}}{p_{1n} - p_{2n}}
 \end{aligned} \tag{8.3.5}$$

$$\begin{pmatrix} p_{1n} \\ p_{2n} \end{pmatrix} = \frac{1}{2} (D_1 x_n^2 + D_2 x_n^2 + e + h) \pm \frac{1}{2} [(D_1 x_n^2 - D_2 x_n^2 + e - h)^2 + 4fg]^{1/2} \tag{8.3.6}$$

where  $u_{on}, v_{on}$  are defined as

$$\begin{aligned} u_{on} &= \int_0^R r u_o(r) J_o(rx_n) dr \\ v_{on} &= \int_0^R r v_o(r) J_o(rx_n) dr. \end{aligned} \quad (8.3.7)$$

From (8.3.6), it is noted that  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) satisfy the equation

$$p^2 - (D_1 x_n^2 + D_2 x_n^2 + e + h)p + (D_1 x_n^2 + e)(D_2 x_n^2 + h) - fg = 0$$

and hence  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive if

$$\min_n (D_1 x_n^2 + e)(D_2 x_n^2 + h) > fg. \quad (8.3.8)$$

If (8.3.8) is satisfied i.e.  $p_{1n}, p_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive,  $u(r, t)$  and  $v(r, t)$  given by (8.3.1) and (8.3.2) take the following forms respectively as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(r, t) = \frac{2}{R} \sum_n x_n \frac{J_o(rx_n)}{J_1(Rx_n)} \left[ \frac{A_n}{p_{1n}} + \frac{B_n}{p_{2n}} \right] \quad (8.3.9)$$

$$\lim_{t \rightarrow \infty} v(r, t) = \frac{2}{R} \sum_n x_n \frac{J_o(rx_n)}{J_1(Rx_n)} \left[ \frac{C_n}{p_{1n}} + \frac{E_n}{p_{2n}} \right]. \quad (8.3.10)$$

It may be verified that the expressions (8.3.9) and (8.3.10) satisfy the steady state form of the system (8.2.6) with boundary conditions (8.2.9). Thus it is seen that the nonstationary solutions (8.3.1) and (8.3.2) tend to the stationary solutions (8.3.9) and (8.3.10) respectively as  $t \rightarrow \infty$ , showing the



asymptotic stability of the equilibrium state provided (8.3.8) holds.

Keeping in view the inequalities (6.2.8) and (8.3.8), it is noted that the stable equilibrium state without dispersal remains so with dispersal. It may also be noted that an otherwise unstable equilibrium state without dispersal can become stable with dispersal under (8.3.8).

Even if the inequality (8.3.8) does not hold, the equilibrium state may become stable provided  $D_1 = D_2$  and the initial and boundary conditions satisfy the following relations

$$(h - \lambda_2) U_1 = fV_1 \quad (8.3.11)$$

$$\text{or} \quad (e - \lambda_2) V_1 = gU_1$$

$$(h - \lambda_2) u_0(r) = f v_0(r) \quad (8.3.12)$$

$$\text{or} \quad (e - \lambda_2) v_0(r) = g u_0(r)$$

where  $\lambda_2$  is given by (6.3.3).

It should be here noted that the above conditions are not applicable to realistic situations.

#### 8.4 STABILITY ANALYSIS WITH DISPERSAL UNDER EFFLUX CONDITIONS

On solving the system (8.2.6) with conditions (8.2.10) in a circular habitat ( $0 \leq r \leq R$ ), we get  $u(r,t)$  and  $v(r,t)$  as

$$u(r, t) = \frac{2}{R} \sum_n I_n(r) \int_0^t [A'_n \exp(-p'_{1n} T) + B'_n \exp(-p'_{2n} T)] dT \\ + \frac{2}{R^2} \sum_n \frac{I_n(r)}{J_0(Ry_n)} [F'_{1n} \exp(-p'_{1n} t) + F'_{2n} \exp(-p'_{2n} t)] \quad (8.4.1)$$

$$v(r, t) = \frac{2}{R} \sum_n I_n(r) \int_0^t [C'_n \exp(-p'_{1n} t) + E'_n \exp(-p'_{2n} T)] dT \\ + \frac{2}{R^2} \sum_n \frac{I_n(r)}{J_0(Ry_n)} [G'_{1n} \exp(-p'_{1n} t) + G'_{2n} \exp(-p'_{2n} t)] \quad (8.4.2)$$

where the summation is taken over all positive roots,  $y_n$ , of the transcendental equation

$$k J_0(Ry) = y J_1(Ry) \quad (8.4.3)$$

and the function  $I_n(r)$  is defined as

$$I_n(r) = \frac{J_0(ry_n)}{J_0(Ry_n)} \frac{y_n^2}{(k^2 + y_n^2)} \quad (8.4.4)$$

The constant coefficients in (8.4.1) and (8.4.2) are given by

$$A'_n = \frac{D_1(p'_{1n} - D_2 y_n^2 - h)U_2 + fD_2 V_2}{p'_{1n} - p'_{2n}} \\ B'_n = \frac{D_1(D_2 y_n^2 + h - p'_{2n})U_2 - fD_2 V_2}{p'_{1n} - p'_{2n}} \\ C'_n = \frac{D_2(p'_{1n} - D_1 y_n^2 - e)V_2 + gD_1 U_2}{p'_{1n} - p'_{2n}} \\ E'_n = \frac{D_2(D_1 y_n^2 + e - p'_{2n})V_2 - gD_1 U_2}{p'_{1n} - p'_{2n}} \quad (8.4.5)$$

$$\begin{aligned}
F'_{1n} &= \frac{(p'_{1n} - D_2 y_n^2 - h) u'_{on} + f v'_{on}}{p'_{1n} - p'_{2n}} \\
F'_{2n} &= \frac{(D_2 y_n^2 + h - p'_{2n}) u'_{on} - f v'_{on}}{p'_{1n} - p'_{2n}} \\
G'_{1n} &= \frac{(p'_{1n} - D_1 y_n^2 - e) v'_{on} + g u'_{on}}{p'_{1n} - p'_{2n}} \\
G'_{2n} &= \frac{(D_1 y_n^2 + e - p'_{2n}) v'_{on} - g u'_{on}}{p'_{1n} - p'_{2n}} \quad (8.4.6)
\end{aligned}$$

$$\begin{pmatrix} p'_{1n} \\ p'_{2n} \end{pmatrix} = \frac{1}{2} (D_1 y_n^2 + D_2 y_n^2 + e + h) \pm \frac{1}{2} [(D_1 y_n^2 - D_2 y_n^2 + e - h)^2 + 4fg]^{1/2} \quad (8.4.7)$$

where  $u'_{on}, v'_{on}$  are defined as follows :

$$\begin{aligned}
u'_{on} &= \int_0^R r u_o(r) J_o(r y_n) dr \\
v'_{on} &= \int_0^R r v_o(r) J_o(r y_n) dr.
\end{aligned} \quad (8.4.8)$$

As in the previous section, it is noted from (8.4.7) that  $p'_{1n}, p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive provided

$$\min_n (D_1 y_n^2 + e) (D_2 y_n^2 + h) > fg. \quad (8.4.9)$$

If (8.4.9) holds, i.e.  $p'_{1n}, p'_{2n}$  ( $n = 1, 2, 3, \dots$ ) are positive, (8.4.1) and (8.4.2) converge to the following forms respectively as  $t \rightarrow \infty$ ,

$$\lim_{t \rightarrow \infty} u(r, t) = \frac{2}{R} \sum_n I_n(r) \left[ \frac{A'_n}{p_{1n}} + \frac{B'_n}{p_{2n}} \right] \quad (8.4.10)$$

$$\lim_{t \rightarrow \infty} v(r, t) = \frac{2}{R} \sum_n I_n(r) \left[ \frac{C'_n}{p_{1n}} + \frac{E'_n}{p_{2n}} \right] . \quad (8.4.11)$$

It may be noted that the expressions (8.4.10) and (8.4.11) satisfy the steady state form of the system (8.2.6) with boundary conditions (8.2.10), showing the asymptotic stability of the equilibrium state. It is concluded from (8.2.8) and (8.4.9) that the equilibrium state which is stable without dispersal remains so with dispersal and also the effect of dispersal is to stabilize even an otherwise unstable equilibrium state under (8.4.9).

Even if (8.4.9) is not satisfied, the equilibrium state can become stable provided  $D_1 = D_2'$ , the initial conditions satisfy the relations (8.3.12) and the boundary conditions satisfy the following relations

$$(h - \lambda_2) U_2 = fV_2 \quad (8.4.12)$$

$$\text{or } (e - \lambda_2) V_2 = gU_2$$

where  $\lambda_2$  is defined in (6.3.3).

## 8.5 CONCLUSION

In circular habitats, effects of dispersal on the linear stability of the equilibrium state of two competing species system with intraspecific interactions and functional response have been investigated under reservoir and flux conditions. It has been asserted from (8.2.8), (8.3.8) and (8.4.9) that the stable equilibrium state without dispersal remains so with dispersal. However, an otherwise unstable equilibrium state without dispersal can become stable with dispersal provided certain inequalities such as (8.3.8), (8.4.9) involving dispersal co-efficients are satisfied. Even if the conditions such as (8.3.8), (8.4.9) are not satisfied, an otherwise unstable equilibrium state may become stable under the following restrictions :

- (i) both the species should have equal dispersal ability i.e.  $D_1 = D_2$ .
- (ii) initial conditions should satisfy the relation (8.3.12).
- (iii) the boundary conditions should satisfy the relations such as (8.3.11), (8.4.12).

Thus it is concluded that dispersal can stabilize even an otherwise unstable equilibrium state provided either certain inequalities involving dispersal co-efficients or certain relations involving initial and boundary conditions are satisfied.

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## CHAPTER IX

### EFFECTS OF DISPERSAL ON STABILITY OF TWO SPECIES SYSTEM WITH MUTUALISTIC INTERACTIONS AND FUNCTIONAL RESPONSE

#### 9.1 INTRODUCTION

In Chapter IV, effects of convective and dispersive migration on the linear stability of the equilibrium state for two species system with mutualistic interactions and functional response have been discussed for constant convective and dispersive co-efficients under non-homogeneous boundary conditions. In this chapter, the effects of variable dispersal co-efficients on both the linear and nonlinear stability of the equilibrium state of the above mentioned system under homogeneous boundary conditions, using Liapunov's Direct Method, have been investigated.

The study related to the nonlinear stability of the equilibrium state for systems of interacting species are of recent origin, Alan Hastings [1], Goh [2], Jorne and Carmi [3], Segel and Levin [6]. Effects of dispersal on the nonlinear stability of the equilibrium state have also been investigated, Alan Hastings [1], Jorne and Carmi [3], Segel and Levin [6]. Eventhough Goh [2] established global stability in a class of prey-predator models including

functional response (Kazarinoff and Driessche [4], Lin and Kahm [5], Segel and Levin [6]), no attempt has been made to study such effects in the case of mutualistic interactions of species (Travis and Post [7], Vandermeer and Boucher [8]). It should be noted here that the effects of dispersive migration have also not been investigated on such interactions.

Keeping the above in view, in the following, we investigate the effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for two species system with mutualistic interactions and functional response under homogeneous boundary conditions.

## 9.2 BASIC EQUATIONS

Consider the mutualistic interactions of two species in a finite ( $0 \leq x \leq L$ ,  $L$  being the length) one dimensional linear habitat. The equations governing their evolution with functional response and dispersal can be written as follows (Lin and Kahm [5], Segel and Levin [6], Travis and Post [7], Vandermeer and Boucher [8]) :

$$\begin{aligned} \frac{\partial N_1}{\partial t} &= N_1(a_1 - a_{11}N_1 + \frac{a_{12}N_2}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_1 \frac{\partial N_1}{\partial x}) \\ \frac{\partial N_2}{\partial t} &= N_2(a_2 - a_{22}N_2 + \frac{a_{21}N_1}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_2 \frac{\partial N_2}{\partial x}) \end{aligned} \quad (9.2.1)$$

where  $N_1(x,t)$ ,  $N_2(x,t)$  represent the population distributions



of two species at time  $t$ ;  $D_1, D_2$  their variable co-efficients of dispersal and are positive. The interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, a_{22}$  and  $\alpha$  are positive constants. The term  $(1+\alpha N_1)^{-1}$  corresponds to the functional response in the model and the constant  $\alpha$  may be interpreted as the measure of the strength of this response (Kazarinoff and Driessche [4]).

The nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (9.2.1) is given by

$$\begin{aligned} a_1 + \frac{a_{12}N_2^*}{1+\alpha N_1^*} &= a_{11}N_1^* \\ a_2 + \frac{a_{21}N_1^*}{1+\alpha N_1^*} &= a_{22}N_2^* \end{aligned} \quad (9.2.2)$$

It can be easily verified from (9.2.2) that there exists only one positive value for  $N_1^*$  and  $N_2^*$  (see Chapter IV).

Writing

$$\begin{aligned} N_1(x, t) &= N_1^* + n_1(x, t) > 0 \\ N_2(x, t) &= N_2^* + n_2(x, t) > 0 \end{aligned} \quad (9.2.3)$$

in the system (9.2.1) and using (9.2.2), we get the following system of nonlinear equations

$$\begin{aligned}
\frac{\partial n_1}{\partial t} &= \frac{(N_1^* + n_1)}{S} \left[ -(a_{11}S + a_{12}\alpha N_2^*)n_1 + a_{12}(1 + \alpha N_1^*)n_2 \right] \\
&\quad + \frac{\partial}{\partial x} \left( D_1 \frac{\partial n_1}{\partial x} \right) \\
\frac{\partial n_2}{\partial t} &= \frac{(N_2^* + n_2)}{S} \left[ a_{21}n_1 - a_{22}Sn_2 \right] + \frac{\partial}{\partial x} \left( D_2 \frac{\partial n_2}{\partial x} \right)
\end{aligned} \tag{9.2.4}$$

where

$$S = (1 + \alpha N_1^*)(1 + \alpha N_1^* + \alpha n_1). \tag{9.2.5}$$

The linearised version of the system (9.2.4) is

$$\begin{aligned}
\frac{\partial n_1}{\partial t} &= -en_1 + fn_2 + \frac{\partial}{\partial x} \left( D_1 \frac{\partial n_1}{\partial x} \right) \\
\frac{\partial n_2}{\partial t} &= gn_1 - hn_2 + \frac{\partial}{\partial x} \left( D_2 \frac{\partial n_2}{\partial x} \right)
\end{aligned} \tag{9.2.6}$$

where  $e, f, g, h$  are positive constants given by

$$\begin{aligned}
e &= N_1^* \left[ a_{11} + \frac{\alpha a_{12} N_2^*}{(1 + \alpha N_1^*)^2} \right], \quad f = \frac{a_{12} N_1^*}{(1 + \alpha N_1^*)} \\
g &= \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2}, \quad h = a_{22} N_2^*.
\end{aligned} \tag{9.2.7}$$

The systems (9.2.4) and (9.2.6) are associated with the following homogeneous boundary conditions:

(i) Flux conditions

$$\begin{aligned}
\frac{\partial n_1}{\partial x}(0, t) &= \frac{\partial n_1}{\partial x}(L, t) = 0 \\
\frac{\partial n_2}{\partial x}(0, t) &= \frac{\partial n_2}{\partial x}(L, t) = 0.
\end{aligned} \tag{9.2.8a}$$

These conditions imply that there is no migration of the species across the boundary of the habitat.

(ii) Reservoir conditions

$$\begin{aligned} n_1(C,t) &= n_1(L,t) = 0 \\ n_2(C,t) &= n_2(L,t) = 0 \end{aligned} \quad (9.2.8b)$$

These conditions suggest that the species populations remain at equilibrium level on the boundary of the habitat.

In the following, we study the linear and nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$  of the system (9.2.1) using Liapunov's Direct Method.

### 9.3 LINEAR STABILITY ANALYSIS

To study the local stability of the equilibrium state in absence of dispersal, the following positive definite function is considered

$$E(n_1, n_2) = \frac{1}{2} (n_1^2 + cn_2^2) \quad (9.3.1)$$

where  $c$  is a positive constant to be chosen suitably. The time derivative of (9.3.1), which on using (9.2.6), becomes

$$\frac{dE}{dt} = -en_1^2 + (f+cg) n_1 n_2 - chn_2^2. \quad (9.3.2)$$

Since  $eh > fg$ , by choosing

$$c = f/g \quad (9.3.3)$$

it may be noted from (9.3.2) that  $\frac{dE}{dt} < 0$  for  $n_1 \neq 0, n_2 \neq 0$  and  $dE/dt = 0$  only when  $n_1 = 0$  and  $n_2 = 0$  ensuring the asymptotic stability of the equilibrium state  $(N_1^*, N_2^*)$ .

To see the effects of dispersal on the linear stability of the equilibrium state, consider the positive definite function

$$E(n_1, n_2) = \frac{1}{2} \int_0^L (n_1^2 + cn_2^2) dx \quad (9.3.4)$$

where  $c$  is chosen as in (9.3.3).

The time derivative of (9.3.4) is

$$\frac{dE}{dt} = \int_0^L (n_1 \frac{\partial n_1}{\partial t} + cn_2 \frac{\partial n_2}{\partial t}) dx \quad (9.3.5)$$

which on substituting (9.2.6) gives

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 - (f+cg)n_1n_2 + chn_2^2] dx \\ & + \int_0^L [n_1 \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) + cn_2 \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x})] dx. \end{aligned} \quad (9.3.6)$$

Integrating the second integral in (9.3.6) and making use of homogeneous boundary conditions (9.2.8), we get

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 - (f+cg)n_1n_2 + chn_2^2] dx \\ & - \int_0^L D_1 \left( \frac{\partial n_1}{\partial x} \right)^2 dx - c \int_0^L D_2 \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \end{aligned} \quad (9.3.7)$$

Since the first integral of (9.3.7) is nonpositive, it is seen that  $\frac{dE}{dt} \leq 0$  and  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ , showing that the equilibrium state is asymptotically stable with dispersal also.

Thus it is concluded that the stable equilibrium state without dispersal remains stable with dispersal as well.

#### 9.4 NONLINEAR STABILITY ANALYSIS

To investigate the nonlinear stability of the equilibrium state in absence of dispersal, consider the positive definite function

$$E(n_1, n_2) = n_1 - N_1^* \ln\left(1 + \frac{n_1}{N_1^*}\right) + c \left[ n_2 - N_2^* \ln\left(1 + \frac{n_2}{N_2^*}\right) \right]$$

$$n_1 > -N_1^*, n_2 > -N_2^* \quad (9.4.1)$$

where  $c$  is a positive constant to be chosen appropriately.

The time derivative of (9.4.1) is

$$\frac{dE}{dt} = \frac{n_1}{N_1^* + n_1} \frac{dn_1}{dt} + \frac{cn_2}{N_2^* + n_2} \frac{dn_2}{dt} \quad (9.4.2)$$

which on using (9.2.4) becomes

$$\frac{dE}{dt} = -\frac{1}{S} (a_{11}S + a_{12}\alpha N_2^*) n_1^2 - ca_{22} n_2^2$$

$$+ [a_{12}(1 + \alpha N_1^*) + ca_{21}] \frac{n_1 n_2}{S} . \quad (9.4.3)$$

By choosing

$$c = \frac{a_{12}}{a_{21}} (1 + \alpha N_1^*) \quad (9.4.4)$$

it is noted from (9.4.3) that  $\frac{dE}{dt} \leq 0$  and  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ . Hence the equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable in the entire positive quadrant  $P = \{(N_1, N_2) | N_1 > 0, N_2 > 0\}$  of the phase-plane.

To examine the effects of dispersal on the nonlinear stability of the equilibrium state, the following positive definite function may be considered

$$E(n_1, n_2) = \int_0^L \left\{ n_1 - N_1^* \ln \left( 1 + \frac{n_1}{N_1^*} \right) + c \left[ n_2 - N_2^* \ln \left( 1 + \frac{n_2}{N_2^*} \right) \right] \right\} dx \quad (9.4.5)$$

where  $c$  is chosen as in (9.4.4).

The time derivative of (9.4.5) is

$$\frac{dE}{dt} = \int_0^L \left[ \frac{n_1}{N_1^* + n_1} \frac{\partial n_1}{\partial t} + \frac{cn_2}{N_2^* + n_2} \frac{\partial n_2}{\partial t} \right] dx \quad (9.4.6)$$

which on using (9.2.4) gives

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L \left\{ (a_{11}S + a_{12}\alpha N_2^*) \frac{n_1^2}{S} + c a_{22}n_2^2 \right. \\ & \left. - [a_{12}(1 + \alpha N_1^*) + ca_{21}] \frac{n_1 n_2}{S} \right\} dx \\ & + \int_0^L \left[ \frac{n_1}{N_1^* + n_1} \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) + \frac{cn_2}{N_2^* + n_2} \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x}) \right] dx. \end{aligned} \quad (9.4.7)$$

Evaluating the second integral in (9.4.7), keeping in view the homogeneous boundary conditions (9.2.8), we get

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L \left\{ (a_{11}S + a_{12}N_2^*) \frac{n_1^2}{S} + c a_{22}n_2^2 \right. \\ & \left. - [a_{12}(1 + \alpha N_1^*) + c a_{21}] \frac{n_1 n_2}{S} \right\} dx \\ & - \int_0^L \frac{D_1 N_1^*}{(N_1^* + n_1)^2} \left( \frac{\partial n_1}{\partial x} \right)^2 dx - c \int_0^L \frac{D_2 N_2^*}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \end{aligned} \quad (9.4.8)$$

Since the first integral is nonpositive, it may be noted from (9.4.8) that  $\frac{dE}{dt} < 0$  for  $n_1 \neq 0, n_2 \neq 0$ ;  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ . Hence the equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable in the entire positive quadrant  $P$  of the phase-plane.

Thus it is concluded that the nonlinearly asymptotically stable equilibrium state without dispersal remains so with dispersal.

## 9.5 CONCLUSION

Using Liapunov's Direct Method, effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for system of two interacting species with mutualistic interactions and functional response have been investigated. It has been shown that the equilibrium state is asymptotically stable in the entire positive quadrant of the phase-plane with or without dispersal.

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## CHAPTER X

### EFFECTS OF DISPERSAL ON STABILITY OF PREY-PREDATOR SYSTEM WITH FUNCTIONAL RESPONSE

#### 10.1 INTRODUCTION

In Chapter V, the linear stability of the equilibrium state for prey-predator system with functional response has been studied by considering the effects of convective and dispersive migration and solving the linearised equations under non-homogeneous boundary conditions. In the present chapter, we study the linear and nonlinear stability of the above system under homogeneous boundary conditions, using Liapunov's Direct Method, as in the case of mutualistic interactions studied in Chapter IX. The domain of attraction of the equilibrium state is also estimated.

In recent years, a great deal of attention has been devoted to the study of nonlinear stability of systems of interacting species and sufficient conditions have been established for the nonlinear stability of the equilibrium state by considering temporal variations of the species, Alan Hastings [1], Gatto and Rinaldi [5], Goh [6,8,9], Goh and Agnew [7], Hsu [11]. In particular, Gatto and Rinaldi [5] considered a generalized prey-predator Lotka-Volterra model and studied the stability properties of its

non-trivial equilibrium state by means of an energy function first proposed by Volterra in the context of conservative ecosystems. Hsu [11] presented certain criteria for nonlinear stability of the locally stable equilibrium state. Effects of dispersal on the nonlinear stability of the equilibrium state have also been investigated, Alan Hastings [2], Jorne and Carmi [12], Rosen [15]. In particular, Jorne and Carmi [12] considered the diffusive Lotka-Volterra system of equations with a number of interacting species and concluded that the diffusive system with zero flux boundary conditions is stable for different positive dispersal co-efficients and the role of diffusion is to dampout all spatial variations. Eventhough Goh [9] has established nonlinear stability in prey-predator system with functional response (Holling [10], Lin and Kahn [14]), the effects of dispersal on the nonlinear stability of such systems have not been investigated.

Keeping these in view, in the following, we examine the effects of variable dispersal co-efficients on the linear and nonlinear stability of prey-predator system with functional response.

## 10.2 BASIC EQUATIONS

Consider the interactions of two dispersive species constituting prey-predator system in a linear one dimensional finite habitat ( $0 \leq x \leq L$ ,  $L$  being the length) with intraspecific

interactions of prey and functional response. The dynamical equations governing their evolution with dispersal along x-direction can be written as follows (Kazarinoff and Driessche [13], Lin and Kahn [14], Jorne and Carmi [12], Segel and Levin [16])

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1(a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_1 \frac{\partial N_1}{\partial x}) \\ \frac{\partial N_2}{\partial t} &= N_2(-a_2 + \frac{a_{21}N_1}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_2 \frac{\partial N_2}{\partial x})\end{aligned}\tag{10.2.1}$$

where  $N_1(x,t)$ ,  $N_2(x,t)$  are population distributions of prey and predator species, respectively, at time  $t$ ;  $D_1, D_2$  their positive variable dispersal co-efficients. The interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}$  and  $\alpha$  are positive constants. The functional response in the model is characterized by the term  $(1+\alpha N_1)^{-1}$  where  $\alpha$  measures the strength of the response (Kazarinoff and Driessche [13]).

The nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (10.2.1) is given by

$$\begin{aligned}a_1 - a_{11}N_1^* - \frac{a_{12}N_2^*}{1+\alpha N_1^*} &= 0 \\ a_2 - \frac{a_{21}N_1^*}{1+\alpha N_1^*} &= 0\end{aligned}\tag{10.2.2}$$

which on solving gives

$$N_1^* = \frac{a_2}{a_{21}-a_2\alpha}; \quad N_2^* = \frac{a_{21}}{a_{12}} \frac{[a_1(a_{21}-a_2\alpha) - a_2a_{11}]}{(a_{21}-a_2\alpha)^2}. \quad (10.2.3)$$

It is noted from (10.2.3) that both  $N_1^*$  and  $N_2^*$  are positive provided

$$a_1(a_{21}-a_2\alpha) > a_2a_{11}. \quad (10.2.4)$$

To investigate the stability of the equilibrium state  $(N_1^*, N_2^*)$ , writing

$$\begin{aligned} N_1(x, t) &= N_1^* + n_1(x, t) > 0 \\ N_2(x, t) &= N_2^* + n_2(x, t) > 0 \end{aligned} \quad (10.2.5)$$

in the system (10.2.1) and keeping in view (10.2.2), we get the following system of non-linear equations

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= \frac{(N_1^* + n_1)}{S} [(a_{12}\alpha N_2^* - a_{11}S)n_1 - a_{12}(1 + \alpha N_1^*)n_2] + \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) \\ \frac{\partial n_2}{\partial t} &= \frac{(N_2^* + n_2)}{S} a_{21}n_1 + \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x}) \end{aligned} \quad (10.2.6)$$

where

$$S = (1 + \alpha N_1^*)(1 + \alpha N_1^* + \alpha n_1). \quad (10.2.7)$$

The linear system corresponding to (10.2.6) is

$$\frac{\partial n_1}{\partial t} = -en_1 - fn_2 + \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) \quad (10.2.8)$$

$$\frac{\partial n_2}{\partial t} = gn_1 + \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x})$$

where

$$e = \frac{N_1^*}{(1+\alpha N_1^*)} \frac{[a_{11}(a_{21}+a_2\alpha)-a_1\alpha(a_{21}-a_2\alpha)]}{(a_{21}-a_2\alpha)} \quad (10.2.9)$$

$$f = \frac{a_{12}N_1^*}{(1+\alpha N_1^*)} ; \quad g = \frac{a_{21}N_2^*}{(1+\alpha N_1^*)^2}$$

and  $n_1(x,t)$ ,  $n_2(x,t)$  are small perturbed population distributions.

From (10.2.9), it may be noted that  $f, g$  are positive and  $e$  is positive for  $a_{11} > a_0 \geq 0$  and negative for  $0 < a_{11} < a_0$ , where

$$a_0 = a_1\alpha \frac{(a_{21}-a_2\alpha)}{(a_{21}+a_2\alpha)} \geq 0 \quad \text{for } \alpha \geq 0. \quad (10.2.10)$$

As considered in the previous chapter, the following boundary conditions are associated with the systems (10.2.6) and (10.2.8):

(i) Flux conditions

$$\begin{aligned} \frac{\partial n_1(0,t)}{\partial x} &= \frac{\partial n_1(L,t)}{\partial x} = 0 \\ \frac{\partial n_2(0,t)}{\partial x} &= \frac{\partial n_2(L,t)}{\partial x} = 0. \end{aligned} \quad (10.2.11a)$$

The boundary conditions (10.2.11a) represent the fact that the population is confined within the region and there is no migration across the boundary.

(ii) Reservoir conditions

$$\begin{aligned} n_1(0,t) &= n_1(L,t) = 0 \\ n_2(0,t) &= n_2(L,t) = 0 \end{aligned} \quad (10.2.11b)$$

These conditions imply that the species populations at the boundary are equal to their equilibrium values.

In the forthcoming sections, using Liapunov's Direct Method, we investigate the stability of the equilibrium state  $(N_1^*, N_2^*)$  under (10.2.4).

### 10.3 LINEAR STABILITY ANALYSIS

To examine the linear stability of the equilibrium state in absence of dispersal, consider the positive definite function

$$E(n_1, n_2) = \frac{1}{2} (n_1^2 + cn_2^2) \quad (10.3.1)$$

where  $c$  is a positive constant to be chosen appropriately.

The time derivative of (10.3.1) is

$$\frac{dE}{dt} = n_1 \frac{dn_1}{dt} + cn_2 \frac{dn_2}{dt} \quad (10.3.2)$$

which on using (10.2.8) gives

$$\frac{dE}{dt} = -en_1^2 + (f-cg) n_1 n_2. \quad (10.3.3)$$

Choosing

$$c = f/g \quad (10.3.4)$$

(10.3.3) becomes

$$\frac{dE}{dt} = -en_1^2. \quad (10.3.5)$$

From (10.3.5), it is noted that  $\frac{dE}{dt} < 0$  for  $e > 0$  and  $n_1 \neq 0$ . Defining the set  $R = \{(n_1, n_2) | \frac{dE}{dt} = 0\}$ , it can be easily verified that the origin is the only invariant subset of  $R$  and, therefore, on using the theorem on extent of asymptotic stability (see [3], p 224), it may be noted that the equilibrium state is asymptotically stable provided  $e > 0$ .

To see the effects of dispersal on the linear stability of the equilibrium state, consider the positive definite function

$$E(n_1, n_2) = \frac{1}{2} \int_0^L (n_1^2 + cn_2^2) dx \quad (10.3.6)$$

where  $c$  is chosen as in (10.3.4).

The time derivative of (10.3.6) is

$$\frac{dE}{dt} = \int_0^L \left( n_1 \frac{\partial n_1}{\partial t} + cn_2 \frac{\partial n_2}{\partial t} \right) dx. \quad (10.3.7)$$

Using (10.2.8), (10.3.4) in (10.3.7) and rearranging, we get

$$\frac{dE}{dt} = -e \int_0^L n_1^2 dx + \int_0^L \left[ n_1 \frac{\partial}{\partial x} \left( D_1 \frac{\partial n_1}{\partial x} \right) + cn_2 \frac{\partial}{\partial x} \left( D_2 \frac{\partial n_2}{\partial x} \right) \right] dx. \quad (10.3.8)$$

Evaluating the second integral and making use of the homogeneous boundary conditions (10.2.11), we have

$$\frac{dE}{dt} = -e \int_0^L n_1^2 dx - \int_0^L \left[ D_1 \left( \frac{\partial n_1}{\partial x} \right)^2 + c D_2 \left( \frac{\partial n_2}{\partial x} \right)^2 \right] dx. \quad (10.3.9)$$

It is seen from (10.3.9) that  $\frac{dE}{dt} \leq 0$  for  $e > 0$ ;  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ . Hence  $e > 0$  is the sufficient condition for asymptotic stability of the equilibrium state. Thus it is concluded that an otherwise stable equilibrium state without dispersal remains so with dispersal.

Even if  $e \leq 0$ , we can find certain condition for asymptotic stability of the equilibrium state under homogeneous reservoir conditions (10.2.11b) provided  $D_1$  and  $D_2$  are positive constants. In such a case, using Poincare's inequality (see [4], p 225) in (10.3.9), we get

$$\frac{dE}{dt} \leq -\left(e + \frac{D_1 \pi^2}{L^2}\right) \int_0^L n_1^2 dx - c \frac{D_2 \pi^2}{L^2} \int_0^L n_2^2 dx. \quad (10.3.10)$$

It may be observed from (10.3.10) that  $\frac{dE}{dt} \leq 0$  for

$$\frac{D_1 \pi^2}{L^2} + e > 0 \quad (10.3.11)$$

and  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ .

Hence (10.3.11) gives the sufficient condition for asymptotic stability of the equilibrium state showing that dispersal has stabilizing effect.



## 10.4 NONLINEAR STABILITY ANALYSIS

Consider the following positive definite function to study the nonlinear stability of the equilibrium state in absence of dispersal

$$E(n_1, n_2) = n_1 - N_1^* \ln\left(1 + \frac{n_1}{N_1^*}\right) + c \left[ n_2 - N_2^* \ln\left(1 + \frac{n_2}{N_2^*}\right) \right] \\ n_1 > -N_1^*, n_2 > -N_2^* \quad (10.4.1)$$

where  $c$  is a positive constant to be chosen suitably.

On substituting (10.2.6) in the time derivative of (10.4.1), we have

$$\frac{dE}{dt} = a_{11}\alpha (1+\alpha N_1^*)(N_0 - N_1) \frac{n_1^2}{S} \\ + \left[ ca_{21} - a_{12}(1+\alpha N_1^*) \right] \frac{n_1 n_2}{S} \quad (10.4.2)$$

where

$$N_0 = \frac{a_1\alpha(a_{21}-a_2\alpha) - a_{11}a_{21}}{a_{11}\alpha(a_{21}-a_2\alpha)}. \quad (10.4.3)$$

By choosing

$$c = \frac{a_{12}}{a_{21}} (1+\alpha N_1^*) \quad (10.4.4)$$

the following results are noted from (10.4.2) regarding the regions of stability:

(i) If  $N_0 \leq 0$

$$\text{i.e. } a_{11} \geq \frac{a_1 \alpha}{a_{21}} (a_{21} - a_2 \alpha) \quad (10.4.5)$$

it may be observed that  $\frac{dE}{dt} \leq 0$  in the positive quadrant  $P = \{(N_1, N_2) | N_1 > 0, N_2 > 0\}$  of the original phase-plane. As the origin is the only invariant subset of  $R = \{(n_1, n_2) | \frac{dE}{dt} = 0\}$ , the equilibrium state  $(N_1^*, N_2^*)$  is asymptotically stable in the entire positive quadrant  $P$  under (10.4.5).

It is also remarked from (10.4.5) that it may not hold for a particular set of parameters value constrained by (10.2.4) showing the destabilizing nature of  $\alpha$ .

(ii) If  $N_0 > 0$

$$\text{i.e. } a_{11} < \frac{a_1 \alpha}{a_{21}} (a_{21} - a_2 \alpha) \quad (10.4.6)$$

we can find a subregion  $A = \{(N_1, N_2) | N_1 > N_0 > 0, N_2 > 0\}$  of the positive quadrant containing the equilibrium state, where  $\frac{dE}{dt} \leq 0$ , provided

$$a_{11} > a_1 \alpha \frac{(a_{21} - a_2 \alpha)}{(a_{21} + a_2 \alpha)} \geq 0 \quad (10.4.7)$$

which is also the condition for linear stability i.e.  $e > 0$ . Combining (10.4.6) and (10.4.7), the criteria for asymptotic stability of the equilibrium state in  $A$  is

$$\frac{a_1 \alpha}{a_{21}} (a_{21} - a_2 \alpha) > a_{11} > a_1 \alpha \frac{(a_{21} - a_2 \alpha)}{(a_{21} + a_2 \alpha)} . \quad (10.4.8)$$

Thus it is concluded that if the equilibrium state is linearly stable, then there exists a subregion A in the phase-plane where it is nonlinearly asymptotically stable under (10.4.8).

Further, it is seen from (10.4.8) that it may not valid for a particular set of parameters value, though the inequality (10.2.4) is consistent, showing that the functional response has destabilizing effect.

The effects of dispersal on the nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$  can be studied by considering the positive definite function

$$E(n_1, n_2) = \int_0^L \left\{ n_1 - N_1^* \ln \left( 1 + \frac{n_1}{N_1^*} \right) + c \left[ n_2 - N_2^* \ln \left( 1 + \frac{n_2}{N_2^*} \right) \right] \right\} dx \quad (10.4.9)$$

where  $c$  is chosen as in (10.4.4).

The time derivative of (10.4.9) is

$$\frac{dE}{dt} = \int_0^L \left[ \frac{n_1}{N_1^* + n_1} \frac{\partial n_1}{\partial t} + \frac{cn_2}{N_2^* + n_2} \frac{\partial n_2}{\partial t} \right] dx. \quad (10.4.10)$$

Substituting (10.2.6), (10.4.4) in (10.4.10) and rearranging, we get

$$\begin{aligned} \frac{dE}{dt} = & \int_0^L a_{11} \alpha (1 + \alpha N_1^*) (N_0 - N_1) \frac{n_1^2}{S} dx \\ & + \int_0^L \left\{ \frac{n_1}{(N_1^* + n_1)} \frac{\partial}{\partial x} \left( D_1 \frac{\partial n_1}{\partial x} \right) + c \frac{n_2}{(N_2^* + n_2)} \frac{\partial}{\partial x} \left( D_2 \frac{\partial n_2}{\partial x} \right) \right\} dx. \end{aligned} \quad (10.4.11)$$

Evaluating the second integral of (10.4.11) and keeping in view the homogeneous boundary conditions (10.2.11), we have

$$\begin{aligned} \frac{dE}{dt} = & \int_0^L a_{11} \alpha (1 + \alpha N_1^*) (N_0 - N_1) \frac{n_1^2}{S} dx \\ & - \int_0^L \frac{D_1 N_1^*}{(N_1^* + n_1)^2} \left( \frac{\partial n_1}{\partial x} \right)^2 dx - c \int_0^L \frac{D_2 N_2^*}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \end{aligned} \quad (10.4.12)$$

The following possibilities arise, which are noted from (10.4.12), regarding the regions of stability:

(i) If  $N_0 \leq 0$  i.e. (10.4.5) holds, the equilibrium state is asymptotically stable in the entire positive quadrant  $P$  of the phase-plane.

(ii) If  $N_0 > 0$  and  $N_0 < N_1^*$  i.e. (10.4.8) holds, the equilibrium state is asymptotically stable in the subregion  $A = \{(N_1, N_2) | N_1 > N_0 > 0, N_2 > 0\}$  of the positive quadrant.

(iii) If  $N_0 > N_1^* > 0$ , there exists a subregion  $B = \{(N_1, N_2) | 0 < N_1 \leq N_0, N_2 > 0\}$  of the positive quadrant where the equilibrium state is asymptotically stable under reservoir conditions (for  $D_1, D_2$  positive constants) provided certain inequality involving dispersal coefficients is satisfied as shown below:

In this case, the inequality  $(N_1^* + n_1) \leq N_0$  is used in the second integral of (10.4.12) to get

$$\begin{aligned} \frac{dE}{dt} \leq & - \int_0^L a_{11} \alpha (1 + \alpha N_1^*) (N_1 - N_0) \frac{n_1^2}{S} dx \\ & - \frac{D_1 N_1^*}{N_0^2} \int_0^L \left( \frac{\partial n_1}{\partial x} \right)^2 dx - c D_2 \int_0^L \frac{N_2^*}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \end{aligned} \quad (10.4.13)$$

Using Poincaré's inequality (see [4], p 225) in the second integral of (10.4.13), we get

$$\begin{aligned} \frac{dE}{dt} \leq & - \int_0^L a_{11} \alpha (1 + \alpha N_1^*) (N_1 - N_0) \frac{n_1^2}{S} dx \\ & - \frac{D_1 \pi^2}{L^2} \frac{N_1^*}{N_0^2} \int_0^L n_1^2 dx - c D_2 \int_0^L \frac{N_2^*}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \end{aligned} \quad (10.4.14)$$

It is seen from (10.4.14) that  $\frac{dE}{dt} \leq 0$  in the subregion B provided

$$\frac{D_1 \pi^2}{L^2} \geq a_{11} \alpha \frac{N_0^3}{N_1^*} \quad (10.4.15)$$

ensuring the stabilizing effect of dispersal.

## 10.5 CONCLUSION

Effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for prey-predator system with functional response have been examined using Liapunov's Direct Method. It has been shown that the functional response has destabilizing effect on the equilibrium state.

The following conclusions have also been drawn:

- (i) An otherwise linearly or nonlinearly stable equilibrium state without dispersal remains so with dispersal.
- (ii) If the equilibrium state is linearly stable without dispersal, then there exists a subregion of the positive quadrant in the phase-plane where it is nonlinearly stable with or without dispersal under (10.4.8).
- (iii) Dispersal has stabilizing effect on the linear and nonlinear stability of the equilibrium state as can be noted from conditions (10.3.11) and (10.4.15) respectively.
- (iv) Even if (10.4.8) is not satisfied, still we can find a subregion of the positive quadrant as the region of stability provided certain condition such as (10.4.15) involving dispersal co-efficients holds.

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## CHAPTER XI

### EFFECTS OF DISPERSAL ON STABILITY OF TWO COMPETING SPECIES SYSTEM WITH FUNCTIONAL RESPONSE

#### 11.1 INTRODUCTION

In Chapter VI, effects of convective and dispersive migration on the linear stability of the equilibrium state for two competing species system with functional response have been studied by solving the system of equations analytically under non-homogeneous boundary conditions. It has been assumed that the convective and dispersive co-efficients are positive constants. In this chapter, using Liapunov's Direct Method, effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for two competing species system with functional response are studied under homogeneous boundary conditions.

The nonlinear stability of systems of interacting species have been studied by many investigators with or without dispersal, Alan Hastings [1,2], Gatto and Rinaldi [4], Gilpin [5], Goh [6,8,9], Goh and Agnew [7], Jorne and Carmi [11]. Teramoto et al. [15] have demonstrated that the predation pressure has a stabilizing effect on the community of competitive species by considering

a model of two preys and one predator having switching property of predation. Hallam [10] has presented a model showing that a proto-co-operative species can drive a stable competitive community to extinction. It should be here noted that though Goh [9] has studied the nonlinear stability of prey-predator system with functional response (Kazarinoff and Driessche [12], Lin and Kahn [13]), such investigations have not been carried out in the case of competing species system with or without dispersal.

Keeping these in view, in the following, we investigate the effects of variable dispersal co-efficients on the linear and nonlinear stability of the equilibrium state for two competing species system with functional response under homogeneous boundary conditions.

## 11.2 BASIC EQUATIONS

Consider the evolution of two dispersive species competing for common ecological niche in a linear one dimensional finite ( $0 \leq x \leq L$ ,  $L$  being the length) habitat with intraspecific interactions and functional response. The equations governing their evolution with dispersal along  $x$ -direction can be written as follows (Kazarinoff and Driessche [12], Lin and Kahn [13], Segel and Levin [14]):

$$\begin{aligned}
 \frac{\partial N_1}{\partial t} &= N_1(a_1 - a_{11}N_1 - \frac{a_{12}N_2}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_1 \frac{\partial N_1}{\partial x}) \\
 \frac{\partial N_2}{\partial t} &= N_2(a_2 - a_{22}N_2 - \frac{a_{21}N_1}{1+\alpha N_1}) + \frac{\partial}{\partial x} (D_2 \frac{\partial N_2}{\partial x})
 \end{aligned}
 \tag{11.2.1}$$

where  $N_1(x,t)$ ,  $N_2(x,t)$  are population distributions of two species at time  $t$ ;  $D_1$ ,  $D_2$  are variable dispersal co-efficients of the species and are assumed to be positive. The interaction co-efficients  $a_1, a_2, a_{11}, a_{12}, a_{21}, a_{22}$  and  $\alpha$  are positive constants. The strength of the functional response  $(1+\alpha N_1)^{-1}$  in the system is determined by  $\alpha$  (Kazarinoff and Driessche [12]).

The nontrivial positive equilibrium state  $(N_1^*, N_2^*)$  of the system (11.2.1) is obtained from

$$\begin{aligned}
 a_1 - a_{11}N_1^* - \frac{a_{12}N_2^*}{1+\alpha N_1^*} &= 0 \\
 a_2 - a_{22}N_2^* - \frac{a_{21}N_1^*}{1+\alpha N_1^*} &= 0.
 \end{aligned}
 \tag{11.2.2}$$

When  $\alpha = 0$ , it should be here noted that the nontrivial positive equilibrium state of the system (11.2.1) is stable provided

$$\frac{a_{22}}{a_{12}} > \frac{a_2}{a_1} > \frac{a_{21}}{a_{11}}.
 \tag{11.2.3}$$

In the case  $\alpha > 0$ , for  $N_1^*, N_2^*$  to be positive, from

(11.2.2) and keeping in view (11.2.3), we have

$$\frac{a_2}{a_{21}-a_2\alpha} > \frac{a_1}{a_{11}} > N_1^* \quad (11.2.4)$$

giving

$$a_{21} > a_2\alpha . \quad (11.2.5)$$

It is also noted from (11.2.2) that there exists only one positive value for  $N_1^*$  and  $N_2^*$  under (11.2.3) and (11.2.5).

In this chapter, therefore, we investigate the linear and nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$  of the system (11.2.1) under (11.2.3) and (11.2.5) using Liapunov's Direct Method.

Using the transformations

$$\begin{aligned} N_1(x, t) &= N_1^* + n_1(x, t) > 0 \\ N_2(x, t) &= N_2^* + n_2(x, t) > 0 \end{aligned} \quad (11.2.6)$$

in the system (11.2.1) and keeping in view (11.2.2), we get the following system of nonlinear equations

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= \frac{(N_1^* + n_1)}{S} \left[ -(a_{11}S - a_{12}\alpha N_2^*)n_1 - a_{12}(1 + \alpha N_1^*)n_2 \right] \\ &\quad + \frac{\partial}{\partial x} \left( D_1 \frac{\partial n_1}{\partial x} \right) \end{aligned} \quad (11.2.7)$$

$$\frac{\partial n_2}{\partial t} = (N_2^* + n_2) \left( -\frac{a_{21}n_1}{S} - a_{22}n_2 \right) + \frac{\partial}{\partial x} \left( D_2 \frac{\partial n_2}{\partial x} \right)$$

where

$$S = (1 + \alpha N_1^*) (1 + \alpha N_1^* + \alpha n_1) . \quad (11.2.8)$$

The linearised form of the system (11.2.7) is

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= -en_1 - fn_2 + \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) \\ \frac{\partial n_2}{\partial t} &= -gn_1 - hn_2 + \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x}) \end{aligned} \quad (11.2.9)$$

where  $n_1, n_2$  represent the small perturbed population distributions and

$$\begin{aligned} e &= \frac{N_1^*}{(1 + \alpha N_1^*)} (a_{11} - a_1 \alpha + 2a_{11} \alpha N_1^*) \\ f &= \frac{a_{12} N_1^*}{(1 + \alpha N_1^*)} \\ g &= \frac{a_{21} N_2^*}{(1 + \alpha N_1^*)^2} ; \quad h = a_{22} N_2^* \end{aligned} \quad (11.2.10)$$

which are positive in view of (11.2.3) and (11.2.5).

The systems (11.2.7) and (11.2.9) are associated with the following boundary conditions:

(i) Flux conditions

$$\begin{aligned} \frac{\partial n_1}{\partial x}(0, t) &= \frac{\partial n_1}{\partial x}(L, t) = 0 \\ \frac{\partial n_2}{\partial x}(0, t) &= \frac{\partial n_2}{\partial x}(L, t) = 0 . \end{aligned} \quad (11.2.11a)$$

These conditions imply that there is no migration of the species across the boundary of the habitat.

(ii) Reservoir conditions

$$\begin{aligned} n_1(0,t) &= n_1(L,t) = 0 \\ n_2(0,t) &= n_2(L,t) = 0 \end{aligned} \quad (11.2.11b)$$

These conditions suggest that the species populations remain at equilibrium level on the boundary of the habitat.

### 11.3 LINEAR STABILITY ANALYSIS

To study the linear stability of the equilibrium state  $(N_1^*, N_2^*)$  in absence of dispersal, consider the positive definite function

$$E(n_1, n_2) = \frac{1}{2} (n_1^2 + cn_2^2) \quad (11.3.1)$$

where  $c$  is a positive constant to be chosen suitably.

Using (11.2.9), the time derivative of (11.3.1) can be written as

$$\frac{dE}{dt} = -en_1^2 - (f+cg)n_1n_2 - chn_2^2. \quad (11.3.2)$$

By choosing

$$c = f/g \quad (11.3.3)$$

it may be noted from (11.3.2) that  $\frac{dE}{dt} \leq 0$  provided

$$eh > fg \quad (11.3.4)$$

$$\text{i.e.} \quad a_{22} [a_{11} - \alpha(a_1 - a_{11}N_1^*) + a_{11}\alpha N_1^*] (1 + \alpha N_1^*)^2 > a_{12}a_{21} \quad (11.3.5)$$

and  $\frac{dE}{dt} = 0$  only when  $n_1=0$  and  $n_2=0$ .

Hence (11.3.5) gives the sufficient condition for asymptotic stability of the equilibrium state which is satisfied, in particular, if

$$N_1^* \geq \frac{a_1}{2a_{11}}. \quad (11.3.6)$$

It may be here remarked that the inequality (11.3.5) for  $\alpha > 0$  may not be satisfied, in general, for a particular set of parameters value, even though the inequalities (11.2.3) and (11.2.5) are consistent showing the destabilizing nature of  $\alpha$ .

The effect of dispersal on the linear stability of the equilibrium state is investigated by considering the following positive definite function

$$E(n_1, n_2) = \frac{1}{2} \int_0^L (n_1^2 + cn_2^2) dx \quad (11.3.7)$$

where  $c$  is chosen as in (11.3.3).

The time derivative of (11.3.7) is

$$\frac{dE}{dt} = \int_0^L (n_1 \frac{\partial n_1}{\partial t} + cn_2 \frac{\partial n_2}{\partial t}) dx \quad (11.3.8)$$

which on using (11.2.9) becomes

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 + cm_2^2 + (f+cg) n_1 n_2] dx \\ & + \int_0^L [n_1 \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) + cn_2 \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x})] dx. \end{aligned} \quad (11.3.9)$$

Evaluating the second integral in (11.3.9) and keeping in view the homogeneous boundary conditions (11.2.11), we get

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 + cm_2^2 + (f+cg) n_1 n_2] dx \\ & - \int_0^L D_1 \left(\frac{\partial n_1}{\partial x}\right)^2 dx - c \int_0^L D_2 \left(\frac{\partial n_2}{\partial x}\right)^2 dx. \end{aligned} \quad (11.3.10)$$

If the inequality (11.3.5) holds, it may be noted from (11.3.10) that  $\frac{dE}{dt} < 0$  for  $n_1 \neq 0$ ,  $n_2 \neq 0$ ;  $\frac{dE}{dt} = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ . Hence the asymptotically stable equilibrium state without dispersal remains so with dispersal.

Even if (11.3.5) does not hold, certain condition involving dispersal co-efficients can be found for asymptotic stability of the equilibrium state under homogeneous reservoir conditions (11.2.11b) when  $D_1, D_2$  are positive constants. In such a case, Poincare's inequality (see [3], p 225) may be used in (11.3.10) to get

$$\begin{aligned} \frac{dE}{dt} \leq & - \int_0^L [en_1^2 + (f+cg) n_1 n_2 + cm_2^2] dx \\ & - \frac{D_1 \pi^2}{L^2} \int_0^L n_1^2 dx - \frac{c D_2 \pi^2}{L^2} \int_0^L n_2^2 dx. \end{aligned} \quad (11.3.11)$$



By choosing

$$c = \frac{a_{12}}{a_{21}} (1 + \alpha N_1^*) \quad (11.4.4)$$

it is observed from (11.4.3) that  $\frac{dE}{dt} \leq 0$  in the entire positive quadrant  $P = \{(N_1, N_2) | N_1 > 0, N_2 > 0\}$  of the phase-plane provided

$$a_{22}(1 + \alpha N_1^*) [a_{11} - \alpha(a_1 - a_{11}N_1^*)] \geq a_{12}a_{21} \quad (11.4.5)$$

giving the sufficient condition for asymptotic stability of the equilibrium state  $(N_1^*, N_2^*)$  in the entire positive quadrant  $P$ .

Since  $\frac{a_1}{a_{11}} > N_1^*$  [see (11.2.4)], it is observed that the inequality (11.4.5) may not be satisfied for a particular set of parameters value constrained by (11.2.3) and (11.2.5) showing again the destabilizing nature of  $\alpha$ .

Even if the inequality (11.4.5) does not hold, there exists a subregion  $A = \{(N_1, N_2) | 0 < N_0 < N_1, 0 < N_2\}$  of the positive quadrant in the original phase-plane, in which  $\frac{dE}{dt} \leq 0$ , containing the equilibrium state provided

$$N_1^* > N_0 > 0 \quad (11.4.6)$$

where

$$N_0 = \frac{1}{\alpha} \left[ \frac{a_{12}a_{21}}{a_{22}a_{11}(1 + \alpha N_1^*)} + \frac{\alpha(a_1 - a_{11}N_1^*)}{a_{11}} - 1 \right] \quad (11.4.7)$$

ensuring the asymptotic stability of the equilibrium state  $(N_1^*, N_2^*)$  in  $A$  under (11.4.6).

To investigate the effects of dispersal on the nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$ , the following positive definite function may be considered

$$E(n_1, n_2) = \int_0^L \left\{ n_1 - N_1^* \ln\left(1 + \frac{n_1}{N_1^*}\right) + c [n_2 - N_2^* \ln\left(1 + \frac{n_2}{N_2^*}\right)] \right\} dx \quad (11.4.8)$$

where  $c$  is chosen as in (11.4.4).

The time derivative of (11.4.8) is

$$\frac{dE}{dt} = \int_0^L \left[ \frac{n_1}{N_1^* + n_1} \frac{\partial n_1}{\partial t} + \frac{cn_2}{N_2^* + n_2} \frac{\partial n_2}{\partial t} \right] dx \quad (11.4.9)$$

which on using (11.2.7) gives

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L \left\{ (a_{11}S - a_{12}\alpha N_2^*) \frac{n_1^2}{S} + c a_{22}n_2^2 \right. \\ & \left. + [a_{12}(1 + \alpha N_1^*) + ca_{21}] \frac{n_1 n_2}{S} \right\} dx \\ & + \int_0^L \left[ \frac{n_1}{N_1^* + n_1} \frac{\partial}{\partial x} (D_1 \frac{\partial n_1}{\partial x}) + \frac{cn_2}{N_2^* + n_2} \frac{\partial}{\partial x} (D_2 \frac{\partial n_2}{\partial x}) \right] dx . \end{aligned} \quad (11.4.10)$$

Evaluating the second integral in (11.4.10) and making use of homogeneous boundary conditions (11.2.11), we get

$$\begin{aligned}
\frac{dE}{dt} = & - \int_0^L \{ (a_{11}S - a_{12}cN_2^*) \frac{n_1^2}{S} + ca_{22}n_2^2 \\
& + [a_{12}(1+cN_1^*) + ca_{21}] \frac{n_1n_2}{S} \} dx \\
& - \int_0^L \frac{D_1N_1^*}{(N_1^*+n_1)^2} \left( \frac{\partial n_1}{\partial x} \right)^2 dx - c \int_0^L \frac{D_2N_2^*}{(N_2^*+n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx.
\end{aligned}
\tag{11.4.11}$$

From (11.4.11), the following possibilities regarding the nonlinear stability can be asserted:

(i) If (11.4.5) holds i.e.  $N_0 \leq 0$ , the equilibrium state which is asymptotically stable in the entire positive quadrant  $P$  of the phase-plane without dispersal remains so with dispersal.

(ii) If  $N_1^* > N_0 > 0$  i.e. (11.4.6) is satisfied, the equilibrium state is asymptotically stable in the subregion  $A$  of the positive quadrant even with dispersal.

(iii) If  $N_0 > N_1^* > 0$ , we can find a subregion  $B = \{(N_1, N_2) | 0 < N_1 \leq N_0, 0 < N_2\}$  of the positive quadrant in which the equilibrium state is asymptotically stable under reservoir conditions (for  $D_1, D_2$  positive constants) provided certain inequality involving dispersal co-efficients holds as shown below:

In this case, using the inequality  $(N_1^*+n_1) \leq N_0$  in the second integral of (11.4.11), we have

$$\begin{aligned}
\frac{dE}{dt} \leq & - \int_0^L \{ (a_{11}S - a_{12}\alpha N_2^*) \frac{n_1^2}{S} + ca_{22}n_2^2 \\
& + [a_{12}(1+\alpha N_1^*) + ca_{21}] \frac{n_1 n_2}{S} \} dx \\
& - \frac{D_1 N_1^*}{L^2} \int_0^L \left( \frac{\partial n_1}{\partial x} \right)^2 dx - cD_2 N_2^* \int_0^L \frac{1}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx \quad (11.4.12)
\end{aligned}$$

Further, Poincare's inequality (see [3], p 225) is used in the second integral of (11.4.12) to get

$$\begin{aligned}
\frac{dE}{dt} \leq & - \int_0^L \{ (a_{11}S - a_{12}\alpha N_2^*) \frac{n_1^2}{S} + ca_{22}n_2^2 \\
& + [a_{12}(1+\alpha N_1^*) + ca_{21}] \frac{n_1 n_2}{S} \} dx \\
& - \frac{D_1 \pi^2}{L^2} \frac{N_1^*}{N_0^2} \int_0^L n_1^2 dx - cD_2 N_2^* \int_0^L \frac{1}{(N_2^* + n_2)^2} \left( \frac{\partial n_2}{\partial x} \right)^2 dx. \quad (11.4.13)
\end{aligned}$$

From (11.4.13), it may be noted that  $\frac{dE}{dt} \leq 0$  in the subregion B provided

$$a_{22} \left[ a_{11} + \frac{D_1 \pi^2}{L^2} \frac{N_1^*}{N_0^2} (1 + \alpha N_1^*) - a_{12} \alpha N_2^* \right] \geq a_{12} a_{21} \quad (11.4.14)$$

showing that dispersal has stabilizing effect.

## 11.5 CONCLUSION

Using Liapunov's Direct Method, effects of dispersal on the linear and nonlinear stability of the equilibrium state

for system of two competing species with functional response have been investigated. It has been noted that the functional response has destabilizing effect on the equilibrium state.

The following conclusions are also drawn:

- (i) An otherwise linearly or nonlinearly stable equilibrium state without dispersal remains stable with dispersal as well.
- (ii) There exists a subregion of the positive quadrant in the phase-plane where the equilibrium state is nonlinearly asymptotically stable under (11.4.6).
- (iii) Dispersal has stabilizing effect on the linear and nonlinear stability of the equilibrium state of the system as can be seen from the conditions (11.3.12) and (11.4.14) respectively.
- (iv) Even if (11.4.6) does not hold, still we can find the region of asymptotic stability which is also the subregion of the positive quadrant provided condition such as (11.4.14) involving dispersal co-efficients is satisfied.

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## CHAPTER XII

### EFFECTS OF DISPERSAL ON STABILITY OF GONORRHEA EPIDEMIC MODEL

#### 12.1 INTRODUCTION

In Chapters IV to XI, effects of convective and dispersive migration on the systems of interacting species have been studied by considering functional response. It may be noted that migration can also affect the spread of infectious diseases under various environmental and geographical conditions. One such disease is gonorrhea caused by sexual contacts between males and females. It can be spread from one region to another by migration of either of these species and therefore this aspect is investigated in this chapter.

The spread of infectious diseases has been extensively studied by various investigators considering temporal variations, Aronsson and Mellander [1], Bailey [2,3,4], Cooke and Yorke [7], Cooke [8], Hethcote [9,10,11], Lajmanovich and Yorke [12], Waltman [15], Wichmann [16]. In particular, a mathematical model for gonorrhea has been first developed by Cooke and Yorke [7]. Hethcote [11] used a host-vector model to study the control of gonorrhea. Lajmanovich and Yorke [12] have presented a generalized model for gonorrhea in a

nonhomogeneous population and studied asymptotic properties of its equilibrium. Yorke et al. [17] have pointed out that saturation in a sexually active core population limits the incidence of gonorrhea and this core causes gonorrhea to remain endemic.

Attempts have also been made to study geographical spread of infectious diseases by considering dispersive migration of susceptibles and infectives, Bailey [2], Capasso [5], Capasso and Fortunato [6], Marcati and Pozio [13], Radcliffe [14]. In particular, Capasso and Fortunato [6] studied the asymptotic behavior of a class of reaction diffusion equations related to models for the spatial spread of infectious diseases. Recently, Marcati and Pozio [13] investigated the global behaviour of a vector disease model by considering spatial spread and hereditary effects which may be applicable to growth and spread of malaria. A theoretical expression giving the velocity of propagation for geographical spread of host-vector and carrier borne epidemics has been developed by Radcliffe [14].

Keeping the above in view, in the following, effects of dispersal on the stability of the endemic equilibrium state of the system governing the spread of gonorrhea are investigated using host-vector model.



## 12.2 BASIC EQUATIONS

Consider that the total number of sexually active and promiscuous portion of the population, living in a linear one dimensional finite habitat ( $0 \leq x \leq L$ ) of length  $L$ , consists of two groups viz. susceptibles and infectives. Let  $c_1, c_2$  be the total number of promiscuous males and females respectively and  $N_1(x, t), N_2(x, t)$  be the total number of the corresponding infectives at the point  $x$  and time  $t$  in the habitat. The dynamical equations governing the population distribution of the infectives are given by (Bailey [2,3,4], Capasso [5], Capasso and Fortunato [6], Marcati and Pozio [13], Radcliffe [14])

$$\frac{\partial N_1}{\partial t} = -a_1 N_1 + b_1 (c_1 - N_1) (N_2 + \alpha_1 \frac{\partial^2 N_2}{\partial x^2}) + D_1 \frac{\partial^2 N_1}{\partial x^2} \quad (12.2.1)$$

$$\frac{\partial N_2}{\partial t} = -a_2 N_2 + b_2 (c_2 - N_2) (N_1 + \alpha_2 \frac{\partial^2 N_1}{\partial x^2}) + D_2 \frac{\partial^2 N_2}{\partial x^2}$$

where  $D_1, D_2$  are dispersal co-efficients of the infectives due to self-diffusion and assumed to be positive constants. The constants  $\alpha_1, \alpha_2$  are cross dispersal co-efficients of the infectives,  $a_1, a_2$  denote the rate at which male, female infectives are cured and  $b_1, b_2$  represent the rate of infection of male, female susceptibles respectively.

The endemic equilibrium state  $(N_1^*, N_2^*)$  of the system (12.2.1) is given by

$$N_1^* = \frac{b_1 b_2 c_1 c_2 - a_1 a_2}{a_1 b_2 + b_1 b_2 c_2} ; \quad N_2^* = \frac{b_1 b_2 c_1 c_2 - a_1 a_2}{a_2 b_1 + b_1 b_2 c_1} \quad (12.2.2)$$

which are positive provided

$$b_1 b_2 c_1 c_2 > a_1 a_2 . \quad (12.2.3)$$

To investigate the stability of the equilibrium state  $(N_1^*, N_2^*)$  of the system (12.2.1), using the following transformations

$$\begin{aligned} N_1(x, t) &= N_1^* + n_1(x, t) > 0 \\ N_2(x, t) &= N_2^* + n_2(x, t) > 0 \end{aligned} \quad (12.2.4)$$

the system (12.2.1) can be written in the form

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= -(a_1 + b_1 N_2^* + b_1 n_2) n_1 + f n_2 + D_1 \frac{\partial^2 n_1}{\partial x^2} + f \alpha_1 \frac{\partial^2 n_2}{\partial x^2} \\ &\quad - b_1 \alpha_1 n_1 \frac{\partial^2 n_2}{\partial x^2} \end{aligned} \quad (12.2.5)$$

$$\begin{aligned} \frac{\partial n_2}{\partial t} &= -(a_2 + b_2 N_1^* + b_2 n_1) n_2 + g n_1 + D_2 \frac{\partial^2 n_2}{\partial x^2} + g \alpha_2 \frac{\partial^2 n_1}{\partial x^2} \\ &\quad - b_2 \alpha_2 n_2 \frac{\partial^2 n_1}{\partial x^2} \end{aligned}$$

where

$$f = b_1(c_1 - N_1^*), \quad g = b_2(c_2 - N_2^*) . \quad (12.2.6)$$

It may be noted from (12.2.2) and (12.2.6) that  $f$  and  $g$  are positive constants as  $c_1 > N_1^*$  and  $c_2 > N_2^*$ .

The linearised version of the system (12.2.5) is

$$\begin{aligned}\frac{\partial n_1}{\partial t} &= -en_1 + fn_2 + D_1 \frac{\partial^2 n_1}{\partial x^2} + f\alpha_1 \frac{\partial^2 n_2}{\partial x^2} \\ \frac{\partial n_2}{\partial t} &= gn_1 - hn_2 + D_2 \frac{\partial^2 n_2}{\partial x^2} + g\alpha_2 \frac{\partial^2 n_1}{\partial x^2}\end{aligned}\tag{12.2.7}$$

where

$$e = a_1 + b_1 N_2^*, \quad h = a_2 + b_2 N_1^* \tag{12.2.8}$$

and  $n_1, n_2$  are the perturbed population distributions in the linearised model.

The systems (12.2.5) and (12.2.7) are associated with the following flux boundary conditions

$$\begin{aligned}\frac{\partial n_1}{\partial x}(0, t) = \frac{\partial n_1}{\partial x}(L, t) &= 0 \\ \frac{\partial n_2}{\partial x}(0, t) = \frac{\partial n_2}{\partial x}(L, t) &= 0.\end{aligned}\tag{12.2.9}$$

The boundary conditions (12.2.9) represent the fact that the population is confined within the region and there is no migration across the boundary.

In the following, we study the linear and nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$  under (12.2.3) using Liapunov's Direct Method.

### 12.3 LINEAR STABILITY ANALYSIS

To examine the linear stability of the endemic equilibrium state  $(N_1^*, N_2^*)$  in absence of dispersal, consider the following positive definite function

$$E(n_1, n_2) = \frac{1}{2} (n_1^2 + \beta n_2^2) \quad (12.3.1)$$

where  $\beta$  is a positive constant to be chosen.

The time derivative of (12.3.1) is

$$\frac{dE}{dt} = n_1 \frac{dn_1}{dt} + \beta n_2 \frac{dn_2}{dt} \quad (12.3.2)$$

and which on substituting (12.2.7) becomes

$$\frac{dE}{dt} = -en_1^2 + (f + \beta g)n_1 n_2 - \beta h n_2^2. \quad (12.3.3)$$

Since  $eh > fg$ , by choosing

$$\beta = f/g \quad (12.3.4)$$

it may be noted from (12.3.3) that  $dE/dt < 0$  for

$n_1 \neq 0, n_2 \neq 0$ ;  $dE/dt = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ .

Hence the equilibrium state  $(0, 0)$  [or  $(N_1^*, N_2^*)$  of the original system (12.2.1)] is always asymptotically stable.

The effects of dispersal on the linear stability of the equilibrium state  $(N_1^*, N_2^*)$  is studied by considering the positive definite function

$$E(n_1, n_2) = \frac{1}{2} \int_0^L (n_1^2 + \beta n_2^2) dx \quad (12.3.5)$$

where  $\beta$  is chosen as in (12.3.4).

The time derivative of (12.3.5) is

$$\frac{dE}{dt} = \int_0^L (n_1 \frac{\partial n_1}{\partial t} + \beta n_2 \frac{\partial n_2}{\partial t}) dx \quad (12.3.6)$$

and which, on substitution of (12.2.7), gives

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 - (f + \beta g)n_1 n_2 + \beta h n_2^2] dx \\ & + \int_0^L [D_1 n_1 \frac{\partial^2 n_1}{\partial x^2} + \beta D_2 n_2 \frac{\partial^2 n_2}{\partial x^2} \\ & + f\alpha_1 n_1 \frac{\partial^2 n_2}{\partial x^2} + \beta g\alpha_2 n_2 \frac{\partial^2 n_1}{\partial x^2}] dx. \end{aligned} \quad (12.3.7)$$

The second integral in (12.3.7) is evaluated and making use of flux boundary conditions (12.2.9), we get

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L [en_1^2 - (f + \beta g)n_1 n_2 + \beta h n_2^2] dx \\ & - \int_0^L [D_1 (\frac{\partial n_1}{\partial x})^2 + \beta D_2 (\frac{\partial n_2}{\partial x})^2 \\ & + (f\alpha_1 + \beta g\alpha_2) \frac{\partial n_1}{\partial x} \frac{\partial n_2}{\partial x}] dx. \end{aligned} \quad (12.3.8)$$

Since the first integral is nonpositive, it may be seen from (12.3.8) that  $dE/dt \leq 0$  provided

$$4D_1 D_2 > fg(\alpha_1 + \alpha_2)^2 \quad (12.3.9)$$

and  $dE/dt = 0$  only when  $n_1 = 0$  and  $n_2 = 0$ . Hence (12.3.9) gives the sufficient condition for asymptotic

stability of the equilibrium state in presence of both self and cross dispersal co-efficients of the infectives.

However, when  $\alpha_1 = 0$  and  $\alpha_2 = 0$  i.e. cross dispersal co-efficients of the infectives are zero, the inequality (12.3.9) holds automatically showing that the endemic equilibrium state which is stable without dispersal remains so with self dispersal. Thus, keeping in view of (12.3.9), it may be remarked that cross dispersal of the infectives have destabilizing effect on the equilibrium state of the system and ultimately the entire population may be infected.

#### 12.4 NONLINEAR STABILITY ANALYSIS

The nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$  in absence of dispersal is analysed by considering the positive definite function (12.3.1). Using (12.2.5) in (12.3.2), we get

$$\begin{aligned} \frac{dE}{dt} = & - [a_1 + b_1(N_2^* + n_2)] n_1^2 - \beta [a_2 + b_2(N_1^* + n_1)] n_2^2 \\ & + (f + \beta g) n_1 n_2 \end{aligned} \quad (12.4.1)$$

where  $\beta$  is given in (12.3.4).

Since  $a_1 a_2 = fg$ , it may be seen from (12.4.1) that  $dE/dt \leq 0$  in the feasible region  $A = \{(N_1, N_2) \mid 0 < N_1 \leq c_1, 0 < N_2 \leq c_2\}$  of the phase-plane showing that the equilibrium state  $(N_1^*, N_2^*)$  is nonlinearly asymptotically stable in the entire region  $A$ .

To see the effects of dispersal on the nonlinear stability of the equilibrium state  $(N_1^*, N_2^*)$ , consider the positive definite function (12.3.5). From (12.3.6) and (12.2.5), we have

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L \left[ (a_1 + b_1 N_2^* + b_1 n_2) n_1^2 + \beta (a_2 + b_2 N_1^* + b_2 n_1) n_2^2 \right. \\ & \left. - (f + \beta g) n_1 n_2 \right] dx \\ & + \int_0^L \left[ D_1 n_1 \frac{\partial^2 n_1}{\partial x^2} + \beta D_2 n_2 \frac{\partial^2 n_2}{\partial x^2} + f \alpha_1 n_1 \frac{\partial^2 n_2}{\partial x^2} \right. \\ & \left. + \beta g \alpha_2 n_2 \frac{\partial^2 n_1}{\partial x^2} - b_1 \alpha_1 n_1^2 \frac{\partial^2 n_2}{\partial x^2} - \beta b_2 \alpha_2 n_2^2 \frac{\partial^2 n_1}{\partial x^2} \right] dx \end{aligned} \quad (12.4.3)$$

where  $\beta$  is chosen as in (12.3.4). Evaluating the second integral and making use of flux boundary conditions (12.2.9), we get

$$\begin{aligned} \frac{dE}{dt} = & - \int_0^L \left[ (a_1 + b_1 N_2^* + b_1 n_2) n_1^2 + \beta (a_2 + b_2 N_1^* + b_2 n_1) n_2^2 \right. \\ & \left. - (f + \beta g) n_1 n_2 \right] dx \\ & - \int_0^L \left\{ D_1 \left( \frac{\partial n_1}{\partial x} \right)^2 + \beta D_2 \left( \frac{\partial n_2}{\partial x} \right)^2 \right. \\ & \left. + \left[ f \alpha_1 - 2b_1 \alpha_1 n_1 + \beta (g \alpha_2 - 2b_2 \alpha_2 n_2) \right] \frac{\partial n_1}{\partial x} \frac{\partial n_2}{\partial x} \right\} dx. \end{aligned} \quad (12.4.4)$$

As the first integral is nonpositive, it is noted from (12.4.4) that  $dE/dt \leq 0$  provided

$$4\beta D_1 D_2 > [\alpha_1(f-2b_1n_1)+\beta\alpha_2(g-2b_2n_2)]^2 \quad (12.4.5)$$

which represents the region bounded by pair of straight lines given by

$$2\alpha_1 b_1 n_1 + 2\beta\alpha_2 b_2 n_2 = f\alpha_1 + \beta g\alpha_2 - 2(\beta D_1 D_2)^{1/2} \quad (12.4.6a)$$

$$2\alpha_1 b_1 n_1 + 2\beta\alpha_2 b_2 n_2 = f\alpha_1 + \beta g\alpha_2 + 2(\beta D_1 D_2)^{1/2} \quad (12.4.6b)$$

containing the equilibrium state  $(0,0)$  when the inequality (12.3.9) holds. If we denote the region bounded by the straight lines  $n_1 = -N_1^*, n_2 = -N_2^*, n_1 = c_1 - N_1^*, n_2 = c_2 - N_2^*$  and (12.4.6a) in the phase-plane by  $B$ , then the equilibrium state  $(0,0)$  [or  $(N_1^*, N_2^*)$  of the original system] is asymptotically stable in the region  $B$  provided (12.3.9) and (12.4.5) are satisfied.

Thus it is concluded that if the equilibrium state is linearly stable with dispersal, then a subregion  $B$  of  $A$  can be found in the phase-plane where it is nonlinearly stable under (12.3.9) and (12.4.5).

If the parameters are such that

$$2(\beta D_1 D_2)^{1/2} \geq b_1 \alpha_1 (c_1 + N_1^*) + \beta b_2 \alpha_2 (c_2 + N_2^*) \quad (12.4.7)$$

the straight line (12.4.6a) does not intersect the feasible region  $A$  and in that case the region  $B$  corresponds to  $A$  showing that the equilibrium state is asymptotically stable in the entire feasible region under (12.4.7). As before,



when  $\alpha_1 = 0$  and  $\alpha_2 = 0$  i.e. cross dispersal co-efficients of the infectives are zero, the inequality (12.4.7) is always valid showing that cross dispersal may destabilize the equilibrium state.

## 12.5 CONCLUSION

Using Liapunov's Direct Method, effect of dispersal on the linear and nonlinear stability of the endemic equilibrium state for gonorrhea epidemic model has been investigated. It has been noted that the equilibrium state is nonlinearly asymptotically stable in the entire feasible region of the phase-plane without dispersal.

The following conclusions may also be drawn with dispersal:

- (i) The endemic equilibrium state is asymptotically stable in the feasible region when cross dispersal co-efficients of the infectives are zero. This implies that in absence of cross dispersal co-efficients, the disease is confined to the equilibrium population in the long run as envisaged by Yorke et al. [17].
- (ii) In presence of both self and cross dispersal co-efficients of the infectives, if the equilibrium state is linearly stable with dispersal, then there exists a subregion in the phase-plane where it is nonlinearly stable under (12.3.9) and (12.4.5).

(iii) In presence of both self and cross dispersal co-efficients of the infectives, the equilibrium state is asymptotically stable in the entire feasible region of the phase-plane provided (12.4.7) holds.

It has also been pointed out from the conditions (12.3.9), (12.4.5) and (12.4.7) that the increase in cross dispersal co-efficients of the infectives may lead to infection of the entire population considered.

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